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Floral Morphology
and Systematics of
Lamourouxia
(Scrophulariaceae:
Rhinanthoideae)

WALLACE R. ERNST

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and Systematics of
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ABSTRACT

Ernst, Wallace R. Floral morphology and systematics of *Lamourouxia* (Scrophulariaceae: Rhinanthroideae). *Smithsonian Contributions to Botany*, number 6, 63 pages, 37 figures. 1971.—Relationships among the twenty-six species, having an overall range from northern Mexico to central Peru, are analyzed in regard to pollinators and for insight into the differentiation of the three taxonomic sections of the genus. Four new names are proposed, including a section, two species, and a combination. Two new chromosome numbers are reported. Descriptions for each of the species and a dichotomous key are included.

Errata. Page 43, col. 2: first paragraph under Section II should read "Corollae tubus plus minusve infundibuliformis, non ventricosus subroseus vel lavandulaceus vel magenteus, non rubro-aurantiacus. Stamina dimorpha, omnia fertilia, inferiora, longiora et majora." Page 49, col. 2: transfer first two paragraphs to col. 1, preceding "16. *L. viscosa*."

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Wallace R. Ernst

Floral Morphology and Systematics of *Lamourouxia* (Scrophulariaceae: Rhinanthoideae)

Introduction

Some confusing patterns of similarities and differences among the species of *Lamourouxia* attracted me to this genus. The distribution of floral and vegetative characters seemed almost to be random so that relationships among the species were obscured. Since none of the previous authors dealing with this genus has attempted an explanation, the purpose of this paper is to provide a systematic restructuring of the genus to account for morphological relationships among the species. The main obstacle proved to be that floral and vegetative characters were difficult to correlate for systematic purposes. This forced the decision to concentrate on floral criteria, as these provided the lower morphological denominator for clustering the species into coordinate sections. The flowers of *Lamourouxia* exhibit two distinctive pollination syndromes. This differentiation brings to mind the observation by Ornduff (1969) that "in genera having a diversity of breeding systems, a taxonomy which emphasizes floral characters will be strikingly different from a taxonomic treatment which stresses characters not associated with reproductive methods." Thus, we are confronted with a challenge to compare and evaluate the various merits of systems based primarily on vegetative or on floral characters. In the case of *Lamourouxia*, the contest resolves to choice between characters of low selective value,

since *Lamourouxia* apparently does not depend upon vegetative reproduction, and characters of high selective value.

This paper is based primarily upon comparative morphology of the flowers of *Lamourouxia* and the goal is an objective systematic arrangement of the species which should also facilitate their identification. The necessary first step to its completion was the taxonomic revision comprising the latter portion of this report. With the taxonomy untangled and the species arranged in systematic order, it also seems possible to predict some of the circumstances that were important in the differentiation of the three sections of this genus. To this end, I propose to evaluate in the first portion of this study the taxonomic and the biological significance of floral and vegetative characters by analyzing their distributions among the species and by considering their role in reproduction and evolution. In defense of my taxonomic framework, I shall attempt to show that the most important taxonomic characters also are biologically significant. My conclusions regarding evolution within *Lamourouxia*, as judged from morphological relationships among the species, can be summarized best by the postulates of Ehrlich & Raven (1969) that "selection is both the primary cohesive and disruptive force in evolution . . .," that "populations will differentiate if they are subjected to different selective forces and will tend to remain similar if they are not . . .," and that "it is the local interbreeding population and not the species that is clearly the evolutionary unit of importance."

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The second portion of this paper includes a new sectional name (*Adelphidion*), two new species names (*L. dispar* and *L. parayana*), one new combination (*L. dasyantha*), two new chromosome numbers (*L. longiflora* and *L. viscosa*), descriptions for the 26 species, and a key to their identification. The generic name *Lamourouxia* is a later homonym which only recently was conserved (Ernst, 1968; McVaugh, 1969). Although this genus previously has been revised three times (Bentham, 1846; Robinson & Greenman, 1895; Paray, 1950), none of these revisions represents the diversity now known. Bentham's generic framework was established on the basis of 18 binomials of which only 12 are now recognized as species. Four of the 14 species described since 1846 were collected for the first time between 1952 and 1958.

Strictly herbarium studies provide useful information for taxonomic purposes and insight into the ranges of variability for commonly accepted taxonomic criteria. For curatorial purposes, monographs stressing morphology help to bring forth the correct name for the appropriate specimens. In most problem instances, however, the monographer who deals only with comparative morphology is not in a favorable position to decide whether a species is a good one from a behavioral point of view, and he is at an even greater disadvantage when it comes to guessing at phylogeny. Often as not, his studies must end where the most interesting part of the subject begins. I could readily subscribe to the hypothesis that an understanding of the variation patterns in *Lamourouxia* would depend in large measure upon an understanding of the morphology and behavior of the pollinators. As summarized by Slobodkin for another context (see Ehrlich & Holm, p. 248, 1963), we are left to wonder what the real world is like.

Materials and Methods

This study is based upon 1178 separate collections representing 3025 herbarium specimens for which all label data have been recorded for comparison. These specimens have been studied at, or borrowed from, the following 26 institutions, which are abbreviated according to Lanjouw & Stafleu (1964): A, BH, BM, C, CAS, COL, DS, ENCB, F, G, GH, K, MEXU, MICH, MO, MSC, NY, P, PENN, PH, POM, RSA, TEX, UC, US, WIS. The Escuela National de Ciencias Biologicas, Mexico, D. F., is

abbreviated as ENCB (see *Taxon* 15: 334, 1966). All types and other specimens of *Lamourouxia* at these institutions have been examined and annotated up to 1968. Samples from 133 collections, representing all taxa, were cleared in lactic acid and microscopically compared. Seeds, hairs, and the venation patterns of leaves and flowers were examined. Meiosis was examined in two species (*L. longiflora* and *L. viscosa*) using buds fixed by Dr. D. E. Breedlove in acetic ethanol. The anthers were squashed in acetocarmine and observed in bright field and phase contrast.

TYPIFICATION

The generic name *Lamourouxia* is a later homonym, but was proposed for conservation (Ernst, 1968) and conserved (McVaugh, 1969) since its first application was as a superfluous name in algae and there is no alternative in Scrophulariaceae. The first seven species were published in Humboldt, Bonpland, & Kunth (1818). The authorship of the binomials in this work, *Nova Genera et Species Plantarum*, is a matter of contention among those favoring Kunth (Stearn, 1968) and those supporting Humboldt, Bonpland, & Kunth (Morton, 1969; Stafleu, 1967). The necessity at hand is the bibliographical reference to the place and date of publication of the earliest names in *Lamourouxia*. Since the generic name and constituent binomials were validly published for the purpose of establishing priority within Scrophulariaceae, the precise authorship of the names seems to me of much less importance. I prefer the widely recognized and understood "H.B.K." which readily identifies the important volumes of the *Nova Genera et Species Plantarum*. Little additional glory can now accrue to Kunth by attributing these binomials only to him, or to insist upon the more awkward reference to Kunth in Humboldt, Bonpland, & Kunth.

When Bentham (1846), in the first revision of the genus, created a section *Lamourouxia*, I believe this narrowed the choice for generic lectotype to one of the species in this section. The only original species of the genus included in this section was *L. multifida* HBK., and it does not matter now what the rationale for the sectional name was in 1846. The only species which can at the same time typify the genus *Lamourouxia* and the section *Lamourouxia* is *L. multifida*. The Report of the Committee for Spermatophyta (McVaugh, 1969) found that the only acceptable

lectotype for the conserved generic name is *L. multifida* and I have proceeded on the strength of that recommendation.

The proposal by Thieret (1954) that *L. virgata* HBK. serve as lectotype for the genus was a reasonable choice for a representative species; however, this choice introduced an awkward problem in regard to sectional names and there is neither morphological nor nomenclatural reason why this species must be accepted for lectotype. I advocated (Ernst, 1968) acceptance of Thieret's choice of lectotype because the original generic description in Humboldt, Bonpland, & Kunth seemed to deal more directly with the kind of staminal development represented in that species. The staminal characteristics of *L. multifida* also were covered but rather maladroitly, as the name "L. pinnatifida" was inadvertently substituted for *L. multifida* although the latter name was used in the formal description of the species. If *L. virgata* were retained as lectotype, then Bentham's section Lamourouxia would have to be discarded and a totally different section Lamourouxia, new in description and new in constituent species, would have to be created to accommodate *L. virgata* and its nearest allies.

When Robinson & Greenman (1895) combined Bentham's sections Lamourouxia and Euphrasioides, they chose the second name to represent the section; however, priority must rest with *Lamourouxia*. Selection of lectotype for section Euphrasioides must be from among those species included under that name by Bentham and, of course, this cannot be *L. multifida*. I propose that *L. xalapensis* HBK. serve as lectotype species for section Euphrasioides Bentham. In my system, section Euphrasioides, following the example of Robinson & Greenman, is combined with section Lamourouxia. The remaining species of the genus comprise two sections. I propose that *L. viscosa* HBK. serve as lectotype species for section Hemispadon and that *L. virgata* HBK. serve as type species for a new section Adelphidion.

Following the binomial references in the taxonomic portion of this paper, I have quoted the author's own published phrases or words concerning the type locality, and, when possible, that portion stating the collector and the collector's serial number. This information is the only tangible means for tying the published, and presumably edited, account of the species to a voucher specimen or specimens. Methods of expression have changed and, often as not, these data differ somewhat from those appearing on the

presumed type-specimen label or from current practice. Serial numbers, sometimes supplied later or by someone other than the collector, especially on older collections, are not always indicative of a single gathering, but may be found on specimens taken on different days or from different regions. The collections of Galeotti illustrate this difficult situation and other examples are not rare, but tedious to discuss. Even so, I believe that most botanists base their descriptions on all available material at hand rather than on a single sheet, and that it is unnecessary to designate individual specimens as lectotypes for species names when the type collections are not taxonomically mixed. I have tried to avoid the much abused term "holotype," as I believe this status can be rightfully conferred on a specimen only by the author of a new taxon in his original description. All specimens mentioned have been examined and the duplicates of type collections which I have cited are taxonomic equivalents.

VARIATION

Measurements in the species descriptions are taken from mature organs, the smallest at the left, an average in parentheses, followed by the largest. Averages are from 10 or more measurements. Notable extremes are given in parentheses to the left or right. Miscellaneous herbarium specimens gathered at random seldom are adequate for a standardized measuring technique. Diversity within species probably would seem less extreme and differences between species more distinctive if the measurements could have been taken from strictly equivalent organs in exactly the same state of development. The dichotomous keys to the species, accordingly, are regrettably difficult.

The distributions of the species are given by country, state, or department. Complete data are given for rare, unusual, or problem specimens. For the more common species, only the number of separately numbered collections examined for that area is given in parentheses, excluding duplicates. All specimens mentioned and plotted have been examined.

Acknowledgments

I am very grateful to the curators and directors of institutions where I have studied or borrowed specimens of *Lamourouxia*. Among the many others who have helped me, the following have my special thanks:

D. E. Breedlove, K. V. Flannery, M. E. Hale, Jr., H. Heine, C. V. Morton, A. Skovsted, J. H. Thomas, H. J. Thompson, and J. Roberts.

Systematic Position

The position of *Lamourouxia* in subfamily Rhinan-thoideae ("Rhinanthideae") has remained unchanged since Bentham's (1846) classification of Scrophulariaceae. In a systematic sense this is near the end of the family among genera such as *Bartsia*, *Castilleja*, *Euphrasia*, *Odontites*, *Pedicularis*, and *Rhinanthus*. The criterion for establishing the subfamily, which is clearly evident in the buds of all species of *Lamourouxia*, is the ontogeny of the corolla in which the lower lip enfolds the upper.

Tribal status is less settled, Euphrasieae (Bentham, 1846; Thieret, 1954), Rhinantheae (Wettstein, 1891), and cannot be resolved here without a comprehensive survey of many other genera. It is clear, however, that if *Lamourouxia* and *Rhinanthus* are sufficiently similar to be accommodated within the same tribe the name of the tribe must be Rhinantheae. The significant characters appear to be the galeate shape of the upper lip of the corolla, the frequently connivent anthers, and the hemiparasitic nature of the plants. The term galeate is ellusive in application and, in this case, probably is of little importance. The upper lip of the corolla is conspicuously galeate in the buds of all species but remains so only in *L. brachyantha*. In the others, the upper lip may seem more or less inverted naviculiform, or once the lobes have reflexed, the corolla, even through sheltering the anthers, may seem little

or no more galeate than sympetalous corollas of other families. In five or six species the anthers are exserted and spreading; in most of the others the fully fertile anthers are connivent in pairs by means of shaggy pubescence, and are displayed near the mouth of the corolla. The similarity of the seeds to those of other genera known to be hemiparasitic suggests that *Lamourouxia* also may make use of rootgrafts for nutritional supplements.

Lamourouxia does not seem to have any very close relationship with other Scrophulariaceae in Mexico and Central America which might give rise to a taxonomic confusion. In South America, however, *L. sylvatica* somewhat recalls the genus *Bartsia* L., and *L. virgata* somewhat recalls the genus *Virgularia* Ruiz & Pavon. Taxonomic characters are available to distinguish these genera, however, and nothing is as yet known about biosystematic relationships. The peculiar seed coats which are among the unifying features of *Lamourouxia* are very similar to those of *Virgularia*, suggesting a relatively close relationship while the very different seeds of *Bartsia* suggest a more remote relationship (Figure 1).

Geographical Distribution

The distribution of *Lamourouxia* extends from northern Mexico at about 30° N, 109° W, in the state of Sonora, to western Panama at about 8° 30' N, 80° 30' W. It begins again in Colombia near the Venezuelan border at about 7° 30' N, 73° W, and extends southward to central Peru, near 12° S, 75° W (Figures 2, 3). Twenty-four species occur between northern Mexico and central Panama and

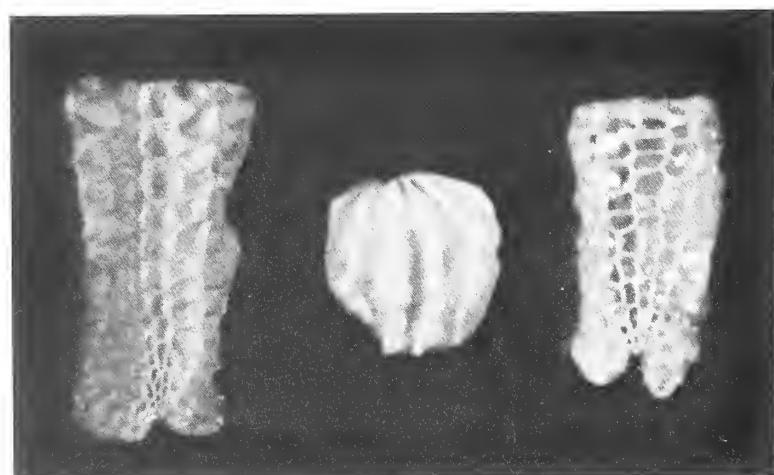


FIGURE 1.—Seed coats of *Lamourouxia* and *Bartsia*, $\times 30$. Center, *Bartsia breviflora*, Ewan 16454, US, showing speroidal shape and ridged surface. Left, *Lamourouxia nelsonii*, Pringle 6777, US, showing characteristic surface, the polygonal depressions are closed by a thin wall. Right, *L. viscosa*, Mexia 1321, US, showing open, polygonal perforations of seed coat.

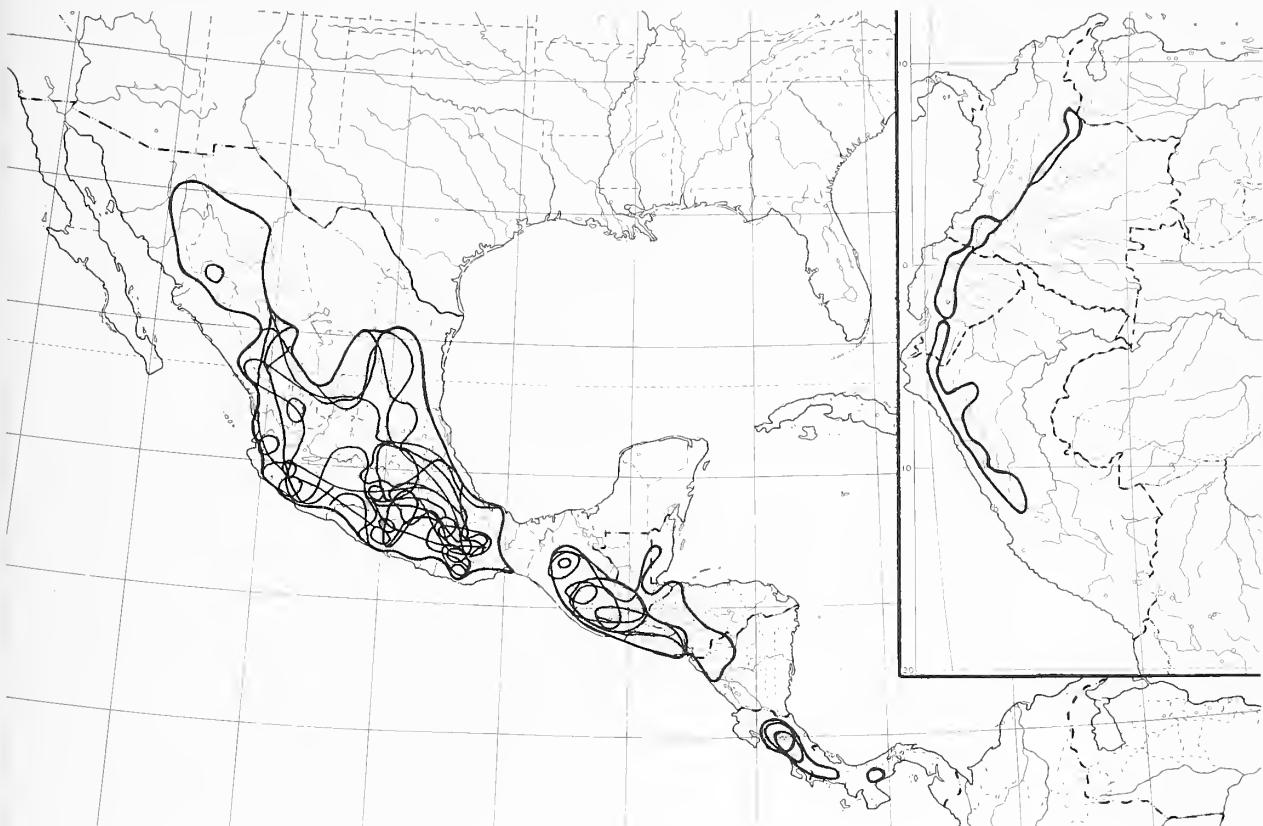


FIGURE 2.—Distributions of twenty-four species of *Lamourouxia* in Mexico and Central America, showing overlapping ranges and discontinuities, compared with distributions of two species in South America spanning Colombia, Ecuador, and Peru.

two species occur in northwestern South America. The most common habitat, at least in Mexico, is openings in or margins of oak and pine forests. At least six species have been collected in or near cultivated areas such as maize fields and hedges; eight species have been collected on limestone or calcareous soil; at least four species have been noted in association with *Acacia* and *Yucca*.

Most collections are from above 1000 m altitude (Figure 4) so that low lands, such as the Isthmus of Tehuantepec and the Isthmus of Panama are important geographical discontinuities (Figure 2). The most common and widespread species also have the greatest altitudinal extremes. The lowest record for the genus is for *L. viscosa* at 450 m in Durango; however, this species also is recorded at 2800 m in Michoacán. The highest record for the genus is *L. multifida* at 3950 m in the state of Mexico, but this species also was collected at 800 m in Sinaloa, indicating an altitudinal range of at least 3000 m. The

low altitude of 500 m for *L. colimae* is notable.

The range of flowering dates (Figure 5) is greater for the more common and widespread species. Three of these, *L. multifida*, *L. virgata*, and *L. viscosa*, apparently flower throughout the year. For the genus as a whole flowering would appear to be most abundant from July through October.

The geographical distributions (Figures 2, 3), particularly for the 20 species in Mexico north of the Isthmus of Tehuantepec, overlap considerably, at least on the scale of this map. Compilations of data from herbarium specimens show, however, that seldom has a collector taken more than one species on the same day and, in these cases, the localities usually appear to be different. A documented exception has been brought to my attention by Dr. D. E. Breedlove who found *L. multifida* (section *Lamourouxia*) and *L. viscosa* (section *Hemispadon*) at a locality in Nayarit and observed the two species being visited by the same pollinators. It is difficult to perceive

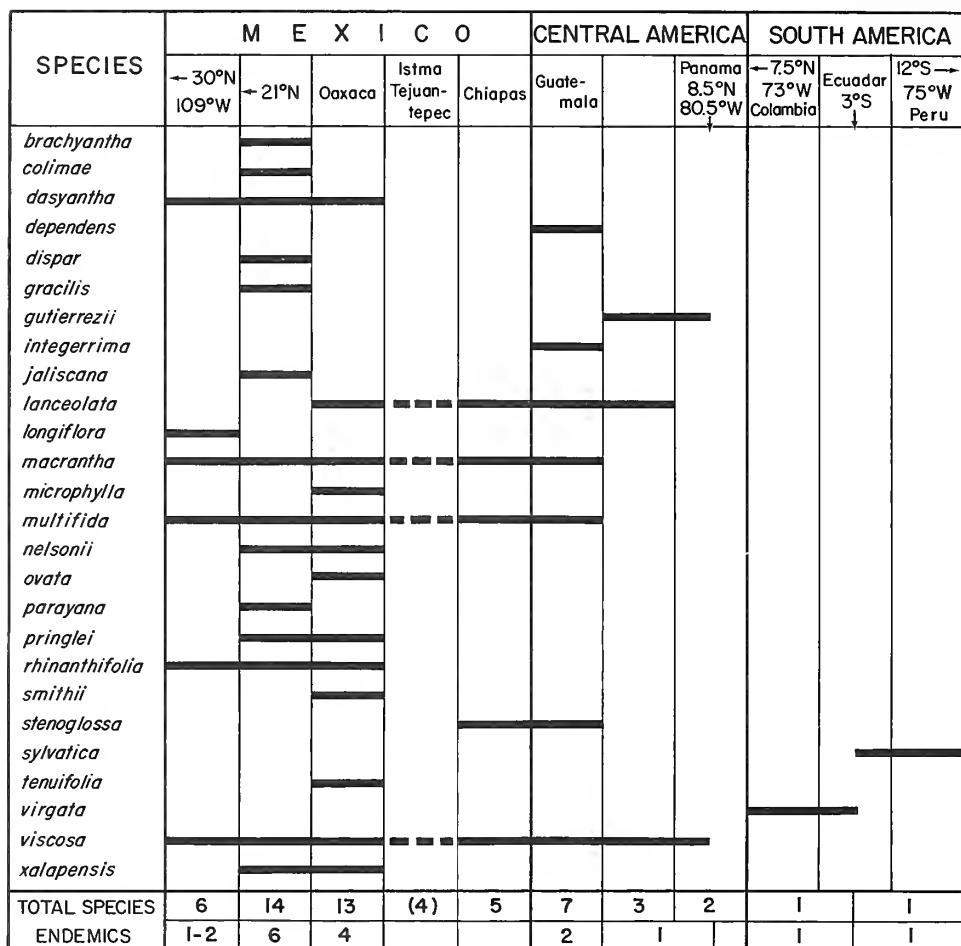


FIGURE 3.—Analysis of geographical distribution of *Lamourouxia*, showing concentration of species in Mexico between 21°N and the Isthmus of Tehuantepec, the four species that cross this Isthmus, and the two geographically separated species in South America.

correlations between geographical distribution patterns and taxonomic characters for the species and sections of this genus. Except for South America, the species and the sections appear to be geographically compatible. Theoretical prerequisites for coexistence of closely related species in the same area have been outlined by Harper et al. (1960). Comprehensive tabulations of altitudinal ranges and of flowering dates (Figures 4, 5) are not helpful for understanding the circumstances in individual situations where plants of different species of *Lamourouxia* might occur side by side. The few species that I have seen in Oaxaca consisted of solitary or a few clustered individuals in widely separated localities. Other col-

lectors sometimes have indicated that the plants were abundant, and Pringle, near the turn of the century, made from 16 to 23 generous duplicates of some rather uncommon species, presumably from single localities.

The two species in South America appear to be mutually exclusive with very little if any geographical overlap, and they are closely allied to two different species occurring in central Mexico. These four species comprise section Adelphidion, which alone has a discontinuous geographical distribution and tends to support "Jordan's Law" pertaining to geographical isolation and speciation (Jordan, 1905; Abrams, 1905; Stebbins, 1950).

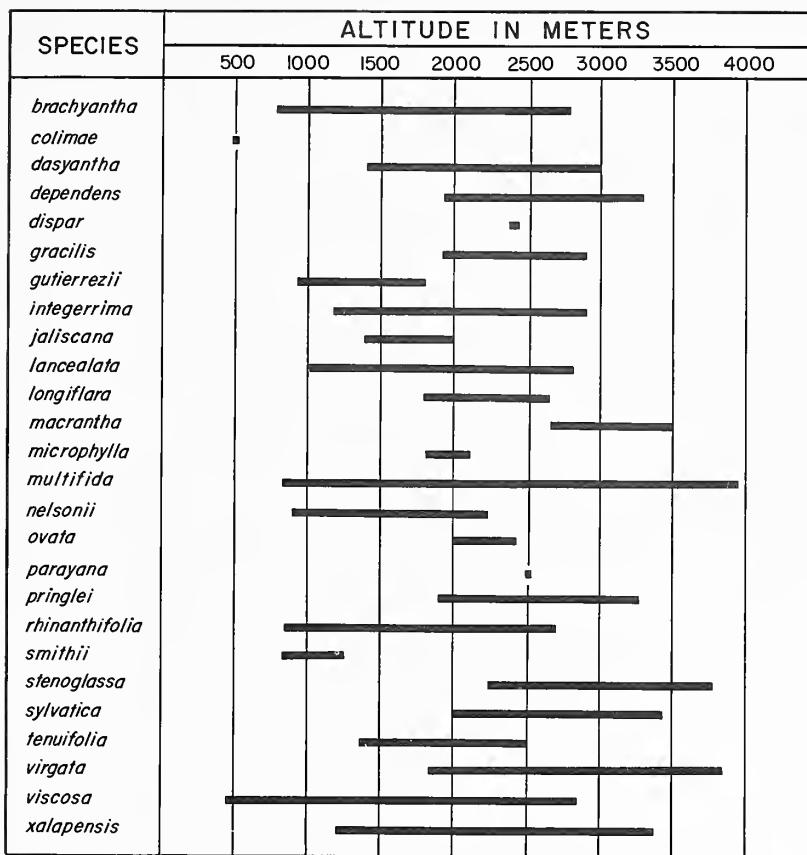


FIGURE 4.—Altitudinal distribution of the species.

Hemiparasitism

Observations and taxonomic conclusions in this paper, particularly in regard to morphological variation and geographical distribution, should be viewed against a somewhat uncertain background of hemiparasitism. The heterotrophic way of life for *Lamourouxia* is implied by the systematic association of this genus with other Rhinanthoid Scrophulariaceae. The similarity of the seed coats (Figure 1) to those of *Orthocarpus* described by Atsatt (1965) and to other known hemiparasites in subfamily Rhinanthoideae also substantiates this opinion. The flowers are attractive, but as there are no records of this genus in cultivation one assumes that the seeds may have special requirements for germination and that the plants are not suited for ordinary garden conditions. The few living plants that I have seen were luxuriantly green and could have been mistaken at first glance for Labiateae. This deceptive appearance prob-

ably explains why so little information on substrates or hosts has been reported on specimen labels.

A review of hemiparasitism in Scrophulariaceae, including illustrations of representative seeds, appears in Kuijt (1969). Experiments and observations by Atsatt (1970b) and by Atsatt & Strong (1970) provide insight into the biology of *Orthocarpus* which also may be applicable, at least in part, to *Lamourouxia*. The only general characteristics of hemiparasites are the ability to form rootgrafts by means of haustoria and the presence of functional chlorophyll; both are assumed to be advantageous. Rootgrafting in *Orthocarpus* can correct some genetic deficiencies, such as restoring chlorophyll synthesis in certain kinds of albino plants, through physiological buffering by host plants (Atsatt, 1970a). Rootgrafts would appear to be formed more or less indiscriminantly between roots of the same individual, from one to another individual of the same species, and to plants of other families in the same community. One, therefore,

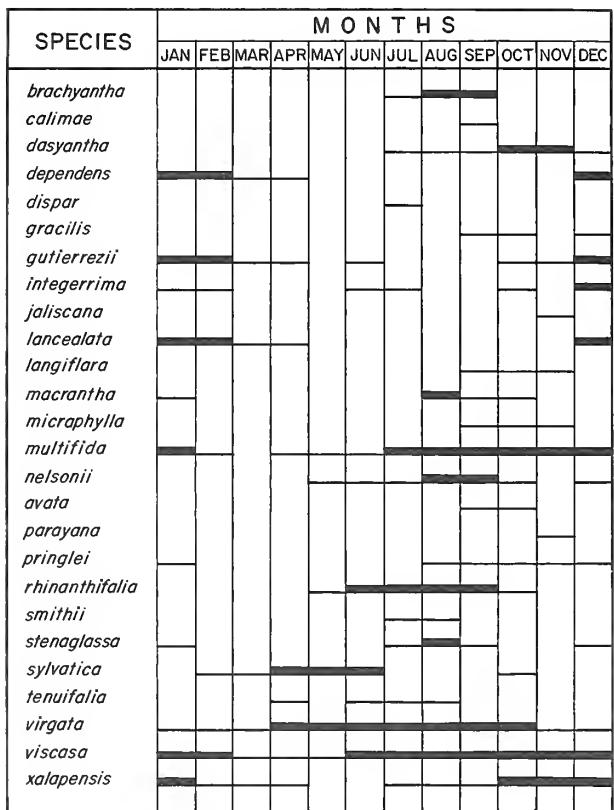


FIGURE 5.—Flowering period of the species with more abundant records represented by thickened lines.

might visualize mixed communities or whole populations of plants that are interconnected and sharing water, mineral, and organic resources. Genetic differences among the plants of *Orthocarpus* range from those capable of independent autotrophic growth to those completely dependent upon hosts. Populations may differ in their heterotrophic and autotrophic capabilities. Survival and reproductive potential mostly are increased when host plants are present. Differences in behavior are to be expected between inbreeding and outbreeding plants of *Orthocarpus*. Facultative hemiparasitism in *Cordylanthus*, a genus allied to *Orthocarpus* and *Castilleja*, has been discussed by Chuang & Heckard (1971).

The ability to form rootgrafts perhaps may expand opportunities for survival and sympatric occurrences in *Lamourouxia* and have taxonomic implications. The standing crop of a species might include side by side plants that are variously out of phase with the regular breeding system and plants that are

optimally functional. Extension of the life expectancy of plants with reduced or marginal fitness, particularly among perennials, probably enriches the genetic and the morphological diversity available for sampling by pollinators as well as by botanical collectors intent upon preparing herbarium specimens. Taxonomists might be well advised to accept broader patterns of variation in superficial vegetative and floral morphology for hemiparasitic plants and, as suggested by Ornduff (1969), strengthen their taxonomic judgments by focusing more attention on understanding reproductive methods.

Vegetative Characteristics

STEMS AND INFLORESCENCES

The stems arise from gnarled burls and probably are somewhat woody below and brittle above, perhaps biennial or perennial. Longer stems may require surrounding vegetation for upright support. Most species are upright, the branching excurrent, the branches diverging at an acute angle, and the inflorescence erect or ascending.

The inflorescences are terminal, indeterminate, racemose, bracteate, and pedicellate. The bracts are more or less leaflike, opposite, decussate, each subtending a solitary pedicel without bracteoles. The flowers thus are paired and often turned so as to appear secund. The inflorescences vary from pubescent to glandular, or glabrous, and are of two kinds. Twenty-two species have ascending inflorescences with erect tips which are associated with excurrent branching. Three species in section *Lamourouxia* (*L. dependens*, *L. ovata*, and *L. xalapensis*) and one species in section *Hemispadon* (*L. lanceolata*) have horizontal or dependent inflorescences with depressed tips which are associated with deliquescent branching. The pedicels in these species are relatively thin and wiry, reflexed away from the apex of the inflorescence, and inverted so that the flowers assume a more or less normal dorsiventral position. Pressed specimens of the latter often appear to have been mounted upside down. Flowers in the species with erect inflorescences may be protandrous while those with dependent inflorescences may be protogynous (Wagner, 1946). These differences in the position of the inflorescences probably are correlated with differences in the breeding system.

LEAVES

The bracts subtending pedicels and the leaves are similar, variable in size and shape, but distinctive and provide characters that are essential for separating the species. The blades of 18 species are rounded or tapered to the base with an indistinct petiole of a millimeter or less in length, yet these are not truly sessile; however, the leaves on the major axes of these species, especially those subtending branches, frequently are quite sessile. Definite petioles of more than a millimeter occur in five species—all of these in section *Lamourouxia*. In strongest contrast, some or all of the leaves of six species are broadly ovate or deltoid, cordate basally, definitely sessile, and more or less clasping. Petiolate and sessile leaves occur in each of the three sections. Many exceptions are found to any generalization about the margin, shape, and size of the leaves.

The margins of the blades are as difficult to describe as the petioles; mostly, they are serrate or nearly so, less often dentate or crenate, and sometimes more or less doubly incised. In many instances the incisions are a blend of two or more states on one plant or on one leaf. Leaf margins in about four species vary from serrate or dentate to crenate; in about six species from serrate or dentate to entire or subentire; in about three species from twice dentate or serrate or crenate; in one species, *L. hyssopifolia* (Figure 16, see *L. longiflora*), with entire, lanceolate blades there are, on rare occasions, from one to three very broad teeth.

The venation is pinnate and craspedodromus with the secondary veins mostly leading directly to the sinus between marginal incisions. The primary and, less often, the secondary veins stand out below (abaxially) and the tertiary veins usually are inconspicuous. Prominent reticulate tertiary veins standing out below usually are characteristic of *L. viscosa*. The venation patterns occasionally are recessed on the upper (adaxial) surface.

The most unusual leaves, those of *L. multifida*, are deeply pinnately divided with several nearly linear or narrowly lanceolate divisions which sometimes are again pinnately parted (Figure 16). Divided leaves also occur in other genera of Scrophulariaceae, as in *Aureolaria*, *Leucospora*, *Macranthera*, and *Seymeria*. The parasitic Scrophulariaceae are the only parasitic Angiosperms having variously divided leaves (Kuijt, p. 82, 1969). The leaves of 20 species of

Lamourouxia are 5 or fewer times as long as broad; 7 species have leaves 6 to 15 times as long as broad. Basal leaves usually are missing from herbarium specimens and there is no indication of juvenile conditions. The leaves are similar to, and grade into, the bracts that subtend the flowers, mostly being larger below and smaller above.

Floral Characteristics

CALYX

The calyx is united, cup-shaped below, and four-lobed (Figure 6). The symmetry varies from nearly regular to very strongly bilabiate; the surface from pubescent, sometimes glandular, to glabrous; the lobes from deltoid to subulate, and from entire to incised. A fifth calyx lobe is rare. A median vein leads to each lobe and one or two veins lead to the sinus, the latter sometimes varying within a species or within a single calyx. When there is one vein it branches at the sinus; when there are two, the veins join just below the sinus and send a branch off to the lobes on either side; thus, each lobe of the calyx receives three veins. The major calyx veins sometimes appear to be overlain externally by a fleshy rib. The axil of the sinus sometimes is revolute, protruding outward like a small lip and sometimes there is an anomalous, small, wartlike appendage situated in the axil (*L. dasyantha*). Characteristics of the calyx often seem to be correlated with those of the leaves and bracts in regard to pubescence, shape, and margin, and may be useful for separating species. In those instances where there are taxonomic problems between similar species, the characteristics of the calyx usually are not helpful. The calyx is persistent and may enlarge somewhat with the maturation of the capsule (Figure 28).

COROLLA

The corollas are horizontal or inclined, bilabiate, bilaterally symmetrical tubes which are variously deformed or ventricose below (Figure 8). All are pubescent externally, sometimes also glandular, and the color of the hairs may contrast with that of the tube; some corollas also may be pubescent internally. During aestivation the lower lip enfolds the upper. Cleared flowers show that the basic venation pattern is 5-merous (Figure 7). Venation in the receptacle

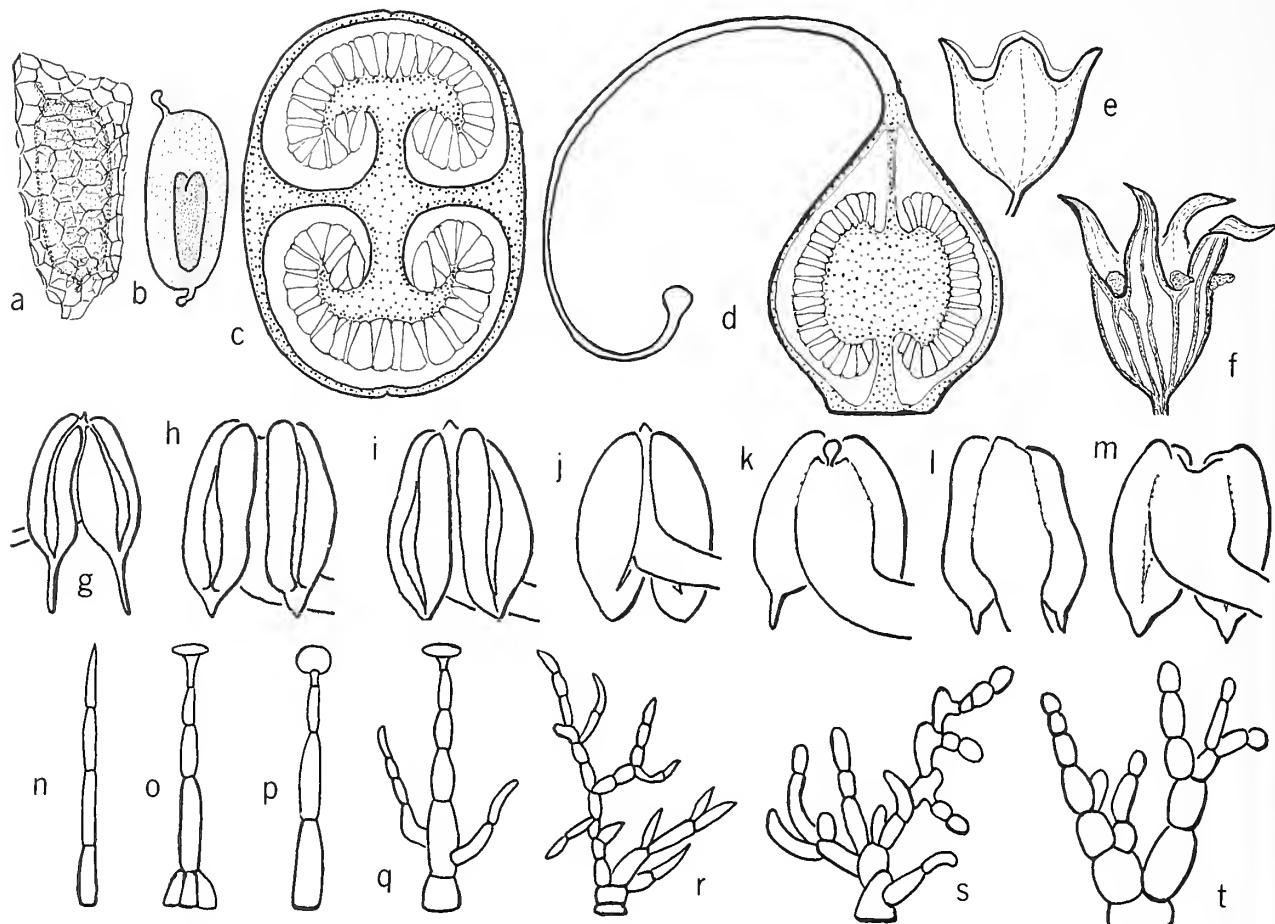


FIGURE 6.—Sample diagrams of floral features. *a*, *L. viscosa*, seed, 1.5 mm long, showing reticulated coat; *b*, same, with endosperm containing embryo removed. *c*, *L. macrantha*, transverse section of young fruit after abscission of corolla showing placentation; *d*, same, longitudinal section, $\times \frac{1}{2}$. *e*, *L. microphylla*, calyx, showing simple venation. *f*, *L. dasyantha*, calyx, showing double and single venation to sinuses with short, anomalous appendages in axiles of sinuses. *g-i*, Introrse views showing diversity in basal mucros of anthers: *g*, *L. multifida*; *h*, *L. gutierrezii*; *i*, *L. dependens*. *j-m*, Extrorse views of anthers showing diversity in connectives: *j*, *L. macrantha*; *k*, *L. virgata*; *l*, *L. tenuifolia*; *m*, *L. nelsonii*. Pubescence not shown on anthers. *n-t*, Typical hairs from middorsal portion of corolla tube except "*o*": *n*, *L. brachyantha*; *o*, same, except from calyx; *p*, *L. multifida*; *q*, *L. viscosa*; *r*, *L. virgata*; *s*, *L. lanceolata*; *t*, *L. microphylla*.

below the insertion of the floral appendages has not been explored. The lips are dissimilar and somewhat different from species to species (Figures 7, 12). The upper lip is more or less two-lobed; the lobes usually are reflexed upward. Whether or not two-lobed, the upper lip always is veined as though two-lobed with each lobe receiving a prominent median vein and a set of lateral veins, all originating independently from the receptacle (Figure 7). Angular, secondary, cross venation unites most of the major veins. The upper

lip at first is galeate, embracing the anthers on the longer filaments. In all but three or four species the upper lip continues to shelter the anthers after anthesis, and in most species, because of the lobing, the upper lip tends to separate the stigma from the anthers. After anthesis the corollas of only *L. brachyantha* remain conspicuously galeate; the others, although always strongly bilabiate and somewhat naviculiform, usually are no more galeate than corollas of other sympetalous families. The upper surface of

the lower lip usually is centrally creased with a groove that leads deep into the corolla chamber. On either side of the crease the lower lip is deformed upward into the palate which is sufficiently large in *L. dasyantha* and *L. sylvatica* to partially or completely occlude the mouth of the corolla.

STAMENS

There are two pairs of stamens (Figure 7). Robinson & Greenman (1895, p. 165) reported a rudimentary fifth stamen but I have never observed one. In some species there may be a few extra veins in the median position of the upper lip of the corolla, the expected position for a fifth stamen; however, these veins appear only to be additional supply to the corolla. The filaments are epipetalous, persistent, and inserted at approximately the same level near the base of the corolla. At their insertion, the filaments usually are swollen, pubescent, probably nectariferous, and frequently somewhat geniculate. Each filament receives one vein from the receptacle. The upper pair of filaments, as the flowers frequently are nearly horizontal, varies from slightly shorter to much shorter than the lower filaments. In 10 species (section Lamourouxia) the 2 sets of filaments are subequal; in 4 species (section Adelphidion) the anthers on the

shorter filaments are smaller but mostly fertile; in 12 species (section Hemispadon) the anthers on the shorter filaments mostly are rudimentary with 1 or 2 unequal locules, usually sterile, or absent (Figures 8, 14). The shorter, upper filaments are inserted below the sinuses separating the lower from the upper lip of the corolla. The longer, lower filaments often are more thickly developed, with somewhat larger anthers and broader connectives, and are inserted below the sinuses between the lobes of the lower lip of the corolla (Figure 7).

Fully fertile anthers are basifixed, usually shaggy pubescent, and bilocular at maturity. The locules are more or less equal in size, completely separated by the connective, laterally dehiscent, and often spurred or mucronate below (Figure 7). The fertile anthers usually are more or less vertical, turned nearly at right angles to the filaments, and face inward in pairs so that corresponding locules are appressed. The meshing of the pubescence in most species appears to hold the introrse anthers pairs together and also to hold or direct the pollen downward and away from the stigma. The larger anthers of most species are usually at least partially visible near or just beyond the mouth in the mature flowers (Figure 8). In some species, long, uniseriate hairs originating on the inside of the corolla become en-

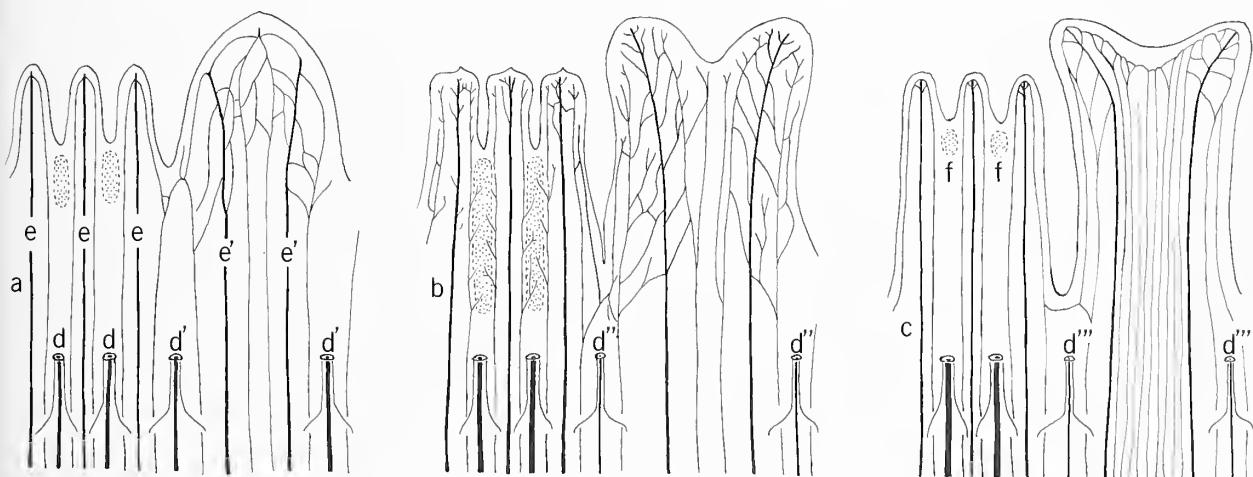


FIGURE 7.—Diagrams of major venation patterns of corollas, reduced to same size, distorted by spreading toward base. *a*, *L. multifida*, based upon Skutch 580, US. *b*, *L. lanceolata*, based upon Skutch 4206, US. *c*, *L. sylvatica*, based upon Pennell & Ferreyra 14924, US. *d*, Fully developed lower stamens; *d'*, fully developed upper stamens; *d''*, small, fertile, upper stamens; *d'''*, rudimentary upper stamens. *e*, Median traces to lower lip; *e'*, main traces to upper lip. *f*, Palate region, stippled.

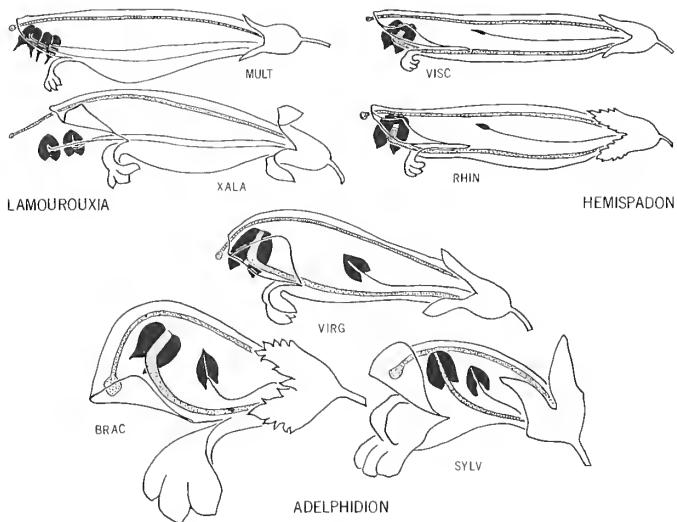


FIGURE 8.—Diagrams of cleared flowers comparing development and position of stamens and stigma in the three sections of *Lamourouxia*. Only one anther of each pair shown; pubescence omitted; $\times 1$, except *L. brachyantha* and *L. sylvatica*, $\times 2$. Left, section Lamourouxia, two pairs of fully developed anthers with subequal filaments; center, section Adelphidion, one pair of large anthers and one pair of smaller anthers; right, section Hemispadon, one large pair of anthers and one pair of sterile filaments.

tangled in the hairs of the anthers, thus partially obstructing the mouth of the corolla and perhaps also holding the anthers in a definite place. The spurs on the lobes of the anthers probably ensure dorsal contact with pollinators; pressure against the spurs probably tends to separate the anthers and to facilitate the downward sifting of the pollen. In three to five species the anthers become exserted and spreading (Figure 21) and lobes of the anthers are more nearly obtuse rather than mucronate. In two species, *L. brachyantha* and *L. sylvatica*, the larger pair of anthers always remains included (Figure 8).

OVARY CAPSULE

The ovary (Figure 6) is two-locular with axile placentation, ovoid, attenuated apically, slightly compressed laterally, and, as the flower lies nearly horizontally, one locule is above, the other below. The ovary sometimes seems to rest upon a solid, short pedicel that at times appears notched and perhaps is secretory; or the ovary is sessile with thickened walls toward the base. A disk has not been observed. The ovary, which only rarely is pubescent, tapers upward into a filiform style which often is sparsely pubescent. The style is situated above the stamens in the horizontal flower and curves distally, pointing the stigma downward just beyond the anthers. Even in the buds the stigma exceeds the stamens. The stigma is delicate and difficult to study in pressed specimens, appearing, at times, conical, clavate, or unequally two-lobed. The delicate, filiform style remains attached to the

ovary as the corolla disengages and falls away. Herbarium specimens frequently show the styles attached to the capsules but this must be of short duration in nature. In some cleared specimens there is a change in the density of the tissues which suggests a predetermined place where the style breaks from the ovary; however, an abscission line has not been observed. The capsules are incompletely loculicidally dehiscent from above, splitting through the base of the style (Figure 24). The capsules are attenuated apically into a flattened and usually crooked beak which is the base of the style (Figure 28).

SEEDS

The ovules are numerous and radiate from the two axile placentae (Figure 6). The seeds are tightly packed, narrower at the base, broader and truncated distally. The shape is more or less irregularly rectangular to oblong, about twice as long as broad (Figure 1). The surface is deeply reticulated, with a lengthwise suture probably associated with the funiculus, and sufficiently translucent to show the opaque, narrowly oblong envelope of endosperm round the small, straight, dicotyledonous embryo (Figure 6). In some but not all samples of seeds from *L. viscosa* the hollows of the reticulated seed coat become open, honeycomblike perforations resembling a loose net around the embryo. These seeds are similar to those of *Orthocarpus densiflorus* described by Atsatt (1965) in his account of a "co-ordinated seed dispersal mechanism" which may be

applicable in part to *Lamourouxia* and to some other Scrophulariaceae. In this case the seeds of *Orthocarpus* at the study site became impaled on the awns of the achenes of *Hypochoeris glabra*, presumably ensuring that the seeds of the hemiparasite and host are together for dispersal and germination. Generally more than one seed of *Orthocarpus* became impaled on the several awns of a given achene of *Hypochoeris*, apparently providing an opportunity for clustering the seeds of the self-incompatible *Orthocarpus* prior to dispersal and germination. The seeds of other species of *Lamourouxia* vary slightly in appearance and the hollows of their reticulated coats are closed by a fragile, porous wall rather than being completely open.

HAIRS

Pubescence, often one of the most conspicuous features of a specimen, nevertheless is difficult to characterize quantitatively for any taxon. Qualitatively, however, the hairs are uniseriate, sometimes arising from a multicellular platform (Figure 6), but otherwise falling into two major categories: simple, and branched or tufted. Both kinds of hairs are sometimes also gland tipped. Grandular hairs are terminated by a globose or flattened gland which usually is on a narrow neck cell. The glands, which may be composed of more than one cell, are difficult to study and are generally similar to the one shown by Wettstein (Pflanzenfam. IV. 3B. (65):42, Fig. 18-C. 1891). Occasionally there are obscure, very minute, sessile or very short stalked or "peltate" glands, also shown by Wettstein (p. 42, Fig. 18-E and F), and by Metcalf & Chalk (p. 980, Fig. 228-C and F. 1950), which seem different and even more difficult to study than the more conspicuous hairs. These minute hairs or glands have been observed on corolla, calyx, and leaves in *Lamourouxia*, but otherwise have been ignored in this present paper.

Simple hairs may occur almost everywhere, but branched or tufted hairs seem only to occur on the corollas. The calyx, bracts, and leaf blades usually agree in characters of pubescence (Table 1). Some specimens, at least, of almost all taxa exhibit caudine pubescence. Those that are abundantly pubescent on leaf and calyx often have conspicuously pubescent stems; those that are glabrate or glabrous may have caudine pubescence confined to paired, narrow, de-

current, internodal strips—the condition that is called bifarious. Organs which seem glabrous sometimes are microscopically pubescent, often in sheltered places such as exiles of serrations on leaf margins, or along the inner margins of calyx lobes, or at the union of the calyx and pedicel.

Excluding the corolla and its internal organs, 10 or 12 species are glabrate to glabrous; most of the pubescent species sometimes are glabrate; 3 species (*L. multifida*, *L. sylvatica*, *L. virgata*) seem to run the gamut from pubescent to glabrous; 4 species (*L. brachyantha*, *L. jaliscana*, *L. nelsonii*, *L. viscosa*) are conspicuously glandular; 4 or 5 additional species are often glandular; 5 species are mostly scabrous; and 3 other species sometimes are scabrous (Table 1). Scabrous hairs appear to be simple, short, often curved or appressed, and with heavily thickened wall. Inconsistent variation in abundance and quality, and whether glandular very seriously limits the systematic and taxonomic usefulness of the hairs, especially on vegetative portions of the plants.

A little additional information can be gleaned from study of the hairs on the corollas when these are compared from closely equivalent areas (Table 1). All corollas are conspicuously, even if not always copiously, pubescent. Branched hairs are thought to be unique to the corollas, and, depending upon the taxon and the place on the corolla examined, branched as well as simple hairs and glandular hairs may occur side by side. Glandular hairs, when they are present, usually are more abundant near the mouth of the corolla. Hairs appearing on the vegetative portions of the plants usually appear more or less white or colorless, although the glands may be dark; however, the corolla hairs usually are darkly or reddish colored.

Even though the hairs on the corolla vary from place to place in structure, appearance, abundance, and in whether glandular, comparisons of the mid-upper portion of the surface of the corolla tube show some similarities which tend to correlate with the clustering of the species. These observations apply only to this region of the corolla tube and, needless to say, no two specimens are exactly the same. The species nearest to *L. multifida*, section Lamourouxia (e.g., those above line 2 in Figure 9), mostly have short, simple hairs, often rather sparse, which frequently terminate in a gland (Figure 6). The species closest to *L. xalapensis* (in the same section, e.g., those species below line 2 in Figure 9),

TABLE 1.—Distribution of hairs with and without glands on mid-upper portion of corolla tube, calyx, and leaves, compared for the three sections of *Lamourouxia*. Exceptions are common in almost every taxon; outstanding exceptions are indicated by the open circles.

| HAIRS | LAMOUROUXIA | | | | | | ADELPHIDION | HEMISPADON | | | | | | | | | | | | | | | | | | |
|--|------------------|-------------------|-----------------|-----------------|---------------|------------------|--------------------|--------------|------------------|-------------------|--------------------|------------------|------------------|----------------|-----------------|----------------|-----------------------|----------------|-----------------|-----------------|--------------------|-------------------|---------------------|-------------------|----------------|--------------------|
| | <i>multifida</i> | <i>longiflora</i> | <i>parayana</i> | <i>pringlei</i> | <i>dispar</i> | <i>macrantha</i> | <i>stenoglossa</i> | <i>ovata</i> | <i>dependens</i> | <i>xalapensis</i> | <i>brachyantha</i> | <i>dasyantha</i> | <i>sylvatica</i> | <i>virgata</i> | <i>nelsonii</i> | <i>viscosa</i> | <i>rhinanthifolia</i> | <i>smithii</i> | <i>jaiscana</i> | <i>gracilis</i> | <i>microphylla</i> | <i>tenuifolia</i> | <i>integriflora</i> | <i>lanceolata</i> | <i>colimae</i> | <i>gutierrezii</i> |
| Mid-upper portion of COROLLA TUBE | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Hairs mostly simple, often <i>glandular</i> | ● | ○ | ● | ● | | | | | | | | | | | | | | | | | | | | | | |
| Hairs mostly branched, arms mostly straight, cells elongated, apex attenuate, mostly <i>not glandular</i> | | | | | ● | ● | ● | ● | ● | ● | | | | | | | | | | | | | | | | |
| Hairs mostly branched, arms straight or curved, mostly <i>not glandular</i> | | | | | | | | | | | ● | ● | ● | ● | | | | | | | | | | | | |
| Hairs for cluster, diverse, mixed, often <i>glandular</i> | | | | | | | | | | | | | | | | | ● | ● | ○ | | | | | | | |
| Hairs mostly intricately branched, often appearing tufted, the cells short, apical cells mostly rounded, mostly <i>not glandular</i> | | | | | | | | | | | | | | | | | | | | ● | ● | ● | ● | ● | ○ | |
| CALYX | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pubescent, mostly <i>not glandular</i> | ○ | ● | | | ● | | | ● | | | | ○ | | | | | ● | ● | ○ | | | | | | | ● |
| Mostly <i>glandular</i> | | ● | ● | ● | | ● | ● | ● | ○ | | ● | | | | | ● | ● | ● | ● | | | | | | | |
| Mostly glabrous or glabrate | | | | | | | | | ● | | ● | ● | ○ | | | | | | ● | ● | ● | ● | ● | ● | ● | |
| LEAVES | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pubescent, mostly <i>not glandular</i> | ● | | ● | | ● | | | ● | | | | ○ | | | | | ● | ● | ● | | | | | | | ● |
| Mostly <i>glandular</i> | | ● | ● | ● | | ● | | ● | | | | ○ | | | | | ● | ● | ● | | | | | | | |
| Mostly glabrous or glabrate | | | | | | | | | ● | | ● | ● | ○ | | | | | | | ● | ● | ● | ● | ● | ● | |
| Mostly scabrous | ○ | | | | ● | ● | | | | | ● | ● | ○ | | | ● | ● | ● | ○ | | | | | | ● | |

mostly tend to have longer hairs with longer, narrow cells; branching is common from below with long, straight arms; glands are very rare or absent and the terminal cell usually is attenuated. It must be noted that in *L. dispar*, section Lamourouxia, the hairs are not glandular, repeatedly branched, tending to be matted, and the cells are relatively short, thus resembling the species below line 2 in Figure 11, section Hemispadon.

The species nearest to *L. viscosa*, section Hemispadon (e.g., most of those above line 2 in Figure 11), are mixed or less easy to characterize. Glandular and nonglandular, simple and branched hairs often stand side by side; branching mostly is from below (Figure 6). The species nearest to *L. lanceolata*, same section (e.g., those below line 2 in Figure 11), are much more distinctive. Glands are absent and the cells tend to be about as long as broad, often appearing like a string of beads, and the terminal cells usually are rounded. These hairs often appear tufted, frequently are intricately branched with short, curving arms, the arms often branching a second time (Figure 6). In this section, Hemispadon, *L. jaliscana* is peculiar since the hairs are usually simple, long, and narrow, with attenuated apexes, some are branched from below, thus recalling species in section Lamourouxia such as *L. xalapensis*. A few hairs also are glandular, somewhat as in *L. multifida*.

The hairs at equivalent positions of the corolla tubes of section Adelphidion lack glands. Those of *L. sylvatica* are straight, relatively long, frequently simple, unbranched, and sparse. Those of *L. brachyantha* are dense, mostly branched from below, and have rather long, straight arms. The hairs of *L. dasyantha* are sparse while those of *L. virgata* (Figure 6) are dense, but otherwise are similar, intricately branched, and the cells and arms are rather short.

The relative selective value of the kinds, abundance, and color of the corolla hairs is by no means clear, especially when simple hairs are contrasted with branched hairs. Pigment or color in the corolla hairs, depending upon their abundance, undoubtedly affects the corolla color and perhaps the attractiveness of the flowers to pollinators. Glandular hairs, especially near the corolla mouth, possibly might discourage some visitors from entering. For systematic purposes, the hairs of the corolla lend support to the clustering of the species. In a few instances they are contradictory as in *L. dispar* and *L. jaliscana*.

Comparative Morphology

Independently of vegetative or other floral characteristics, the species can be clustered objectively to form three sections according to the development of the stamens (Figure 8). The 10 species of section Lamourouxia have 2 pairs of similar anthers; the 12 species of section Hemispadon have 1 pair of anthers and a pair of sterile stamens; the 4 species of section Adelphidion are intermediate with 2 dissimilar pairs of anthers. Shape and color of the corolla are correlated with the development of the stamens so that two pollination syndromes are represented. The flowers of the first two sections have long, narrow, red corollas, and are presumed to be pollinated by hummingbirds (Figures 16, 21, 28, 34). The flowers of the third section have shorter, broader, non-red corollas, and are presumed to be pollinated by bees (Figures 8, 24). The differential development of the stamens provides a morphological series (Figure 14) in which the bee-flowered species appear to be intermediate between the two sections of bird-flowered species and suggests an explanation of how there can be two sections with flowers that are similar in appearance and function.

SECTION LAMOUROUXIA

The flowers in this section have two subequal pairs of stamens (Figure 8). The four, fully fertile anthers are similar in size and shape, inserted on similar filaments, and the lower pair slightly exceeds the upper in length. The corollas are vivid red, and suggest the syndrome of ornithophily (Faegeri & van der Pijl, 1966). These are the unifying characters of this section.

The corollas show two extremes in silhouettes which are correlated with the position of the anthers and with characters of the inflorescences. The tubes of the corollas of *L. multifida*, typical also of *L. longiflora*, *L. parayana*, and *L. pringlei*, are more or less narrowly funnelform, usually conspicuously ventricose, somewhat narrowed at the mouth, and the flowers are displayed in ascending racemes. The larger upper lip shelters the mouth and the four partially exposed, mutually connivent, shaggy, and strongly mucronate anthers. The forward margins of the upper lip are slightly lobed or not lobed, slightly reflexed or not reflexed, and appear more or less inverted naviculiform. The mouth is somewhat obstructed by the

connivent anthers and the narrow, lower lip tends to arch downward abruptly (Figure 16).

The other extreme is exemplified by *L. xalapensis*, which also is typical of *L. dependens* and *L. ovata*. The corollas in this case have tubes more broadly funnelform, not ventricose or only slightly so, sometimes concave below, and they are broadest at the mouth. The rounded lobes of the upper lip are reflexed upward, the anthers are exserted, spreading, less pubescent, and slightly or not mucronate. The broad lower lip usually juts forward with spreading lobes, and the gaping mouth is unobstructed (Figures 8, 21). This latter group of species, including *L. xalapensis*, is remarkable because the inflorescences are depressed or dependent rather than ascending. This appears to be correlated with deliquescent growth and nearly right angle branching. The wiry pedicels permit the flowers to invert, thus assuming the normal dorsiventral position. It would appear that the species closest to *L. xalapensis* differ in some important way from those closest to *L. multifida*. There is a suggestion in a study of hummingbird behavior (Wagner, 1946) that the flowers of "*L. exserta*" (= *L. xalapensis*) are protogynous; thus, one might speculate that the flowers of the first group, including *L. multifida*, with their erect inflorescences, may be protandrous. This, of course, ought to be verified. The dependent inflorescence occurs also in *L. lanceolata* of section Hemispadon.

The intervening species detract from the distinctness of the above two extremes in floral morphology which otherwise could have been separated taxonomically into two sections or subsections of coordinate rank. The distribution of characters in the intervening species (Figure 9) links all of them into a more or less continuous morphological series, so that they seem more like one section. Various combinations of characters suggest a close alliance among *L. macrantha*, *L. ovata*, and *L. dependens*. A taxonomic problem unexpectedly links *L. macrantha* with *L. stenoglossa* in Guatemala. As the name implies, *L. dispar* is enigmatic because some of its characters suggest a relationship with section Hemispadon while others, especially the four subequally developed stamens, indicate a central position within section Lamourouxia. These problems are discussed in the taxonomic portion of this report following the species descriptions.

The distribution of some vegetative characters in section Lamourouxia is shown in Figure 9. Some

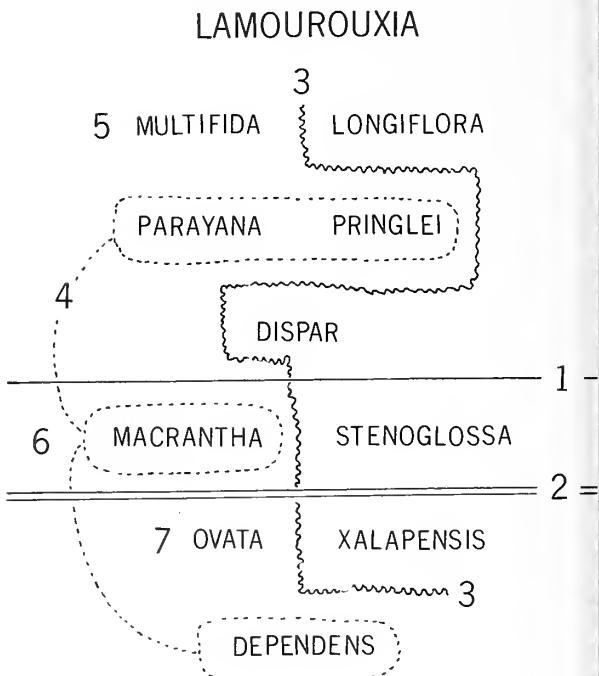


FIGURE 9.—Approximate systematic position of species in section Lamourouxia showing distribution of taxonomic characters. Above line 1 the anthers tend to be mutual connivent and barely exposed in the mouth of the corolla below the line they tend to be exserted and spreading. Above line 2 the plants are upright with excurrent branching and ascending inflorescence tips; below the line the plants are dependent, with deliquescent, often right-angle branching and the inflorescence tips are depressed with corresponding inverted flowers. To the left of line 3 the leaf blades tend to be ovate; to the right lanceolate. Line 4 indicates species tending to have glandularly pubescent calyx and leaves. Species 5 has unique, pinnately divided leaf blades. Species 6 has broadly cordate leaves on short petioles. Species 7 has broadly cordate, sessile leaves.

vegetative characters tend to reinforce the grouping of the species while others only emphasize the diversity within the section. Line 1 divides the species on the basis of characters of the anthers. Line 2 divides them again on the basis of the inflorescence. Line 3 divides the species according to whether the leaves are mostly ovate or mostly lanceolate. Although individual specimens of any of these species may vary from pubescent to glabrate or glabrous, the ones enclosed by line 3 mostly are conspicuously pubescent and the hairs mostly are glandular. The leaves of species 5, *L. multifida*, are exceptional because they have relatively long petioles and the blades are pinnately divided in

narrow segments. The leaves of species 6, *L. macrantha*, are exceptional because they are large, short petiolate, broadly ovate, and deeply cordate at the base. The leaves of species 7, *L. ovata*, are very similar to those of *L. macrantha*, except that they are sessile. All other species in this section are petiolate with the blades rounded or tapered to the base. Although the petioles sometimes are less than a millimeter in length the blades are not truly sessile. Another character, not indicated in the figure, is the distinctive double or irregular leaf margins, which vary in some combinations of serrate-dentate-crenate, for *L. macrantha*, *L. stenoglossa*, *L. ovata*, and *L. dependens*. This character of the leaf margins occurs among relatively interrelated species whose geographical distributions center on the margins of the Isthmus of Tehuantepec (Figure 22). The margins in the other species are simple serrate or dentate or crenate, except for the margins of *L. longiflora* and the margins of the narrow division in *L. multifida*, which are entire. The restricted distribution of *L. longiflora* is contiguous with that of *L. multifida*, and the two are predicted to be relatively closely related (Figure 17).

Six species only occur in Mexico northwest of the Isthmus of Tehuantepec; two species, *L. stenoglossa* and *L. dependens*, only occur on the southeast side of the Isthmus; and two species, *L. multifida* and *L. macrantha*, occur on either side of the Isthmus. The Isthmus of Tehuantepec is particularly notable in regard to the distribution of section Lamourouxia (Figure 3). The three species with dependent inflorescences, *L. dependens*, *L. ovata*, and *L. xalapensis*, have distributions more or less neighboring around this Isthmus, the species being restricted to the one side or to the other (Figure 22). The one species in section Hemispadon with the same inflorescence character, *L. lanceolata*, also shares this distribution but occurs on either side of this Isthmus (Figure 30). A few specimens of *L. dependens* from Guatemala have unusually small calyxes which also tend to be glabrous, thus causing these specimens to be confusingly similar to *L. xalapensis* which only occurs to the west of the Isthmus. West of the Isthmus, *L. macrantha* is among the most distinctive species; to the east, especially in Chiapas, *L. stenoglossa* is remarkably distinctive. Both of these species also occur in Guatemala, where their distinguishing characters appear to become blended in some specimens (Figure 22).

SECTION ADELPHIDION

The stamens in this section are dimorphic (Figure 8). The longer pair have thicker filaments and larger anthers which are pubescent and mucronate. The upper pair are half or two-thirds as long, the filaments are thinner, the anthers smaller, less pubescent, attenuate basally, always included, mostly two-locular at anthesis, and usually fertile. The corollas are pink, lavender, exceptionally magenta, purple or white, and suggest the syndrome of melittophily (Faegeri & van der Pijl, 1966). The tubes tend to be broadly funnel-form, broadest toward the mouth, and slightly or not at all ventricose, with the lobes of the lips generally broadly rounded, and the mouths relatively large, although mostly occluded by large palates in two species. These are the unifying characters of this section (Figure 24).

Several characters clearly mark *L. brachyantha* as exceptional. The development of the stamens and the color of the corolla are the reasons for placing it in the new section Adelphidion where it seems remote from the other species. The corollas are conspicuously galeate with a large, open, downward-facing mouth. The large pair of anthers is included and the stigma is slightly or not at all exposed.

The corolla mouths are relatively large in the remaining three species but almost or completely obstructed by the large palate in *L. sylvatica* and *L. dasyantha*, and less so in *L. virgata*. The large pair of anthers and their thickened filaments are partially exposed in the mouth of *L. virgata*, thus recalling section Hemispadon. The large anthers usually are less exposed in *L. dasyantha* and included in *L. sylvatica*. The stigma is exposed in *L. virgata* and *L. dasyantha*, but little or rarely exposed in *L. sylvatica*. The tendency for included anthers and the non-red corollas of *L. brachyantha*, *L. sylvatica*, and *L. dasyantha* suggest the syndrome of melittophily in which the pollinators bodily enter the corolla chamber. The corollas of *L. virgata* usually are longer and sometimes approach red in color. The morphology of the corollas of *L. virgata*, more than any other species, suggest that they may be pollinated by bees as well as by birds. The small included pair of anthers in *L. virgata* mostly are bilocular and fertile, but occasionally they are rudimentary and sterile, again recalling characters of section Hemispadon.

The distribution of vegetative characters in section

Adelphidion (Figure 10) is less instructive because there are so few species to examine. Two distinctive features characterize *L. brachyantha*: the leaves are broadly ovate, cordate, sessile, and clasping, and the plants are densely glandular pubescent. This combination of characters recalls some species in section *Hemispadon*, and probably influenced Greenman (1905) to place *L. brachyantha* next to *L. rhinanthifolia*. The leaves of the remaining species in section *Adelphidion* mostly are lanceolate, narrowed to the base, mostly glabrate, and not glandular. The leaves on the main axis, particularly those subtending branches, are sessile. A number of exceptions occur in *L. sylvatica* where the leaves sometimes are broadly lanceolate to ovate, occasionally pubescent, and rarely the hairs are glandular. Plants of *L. dasyantha* frequently are well branched from near the base, and sometimes are described as tufted in appearance.

Two quite dissimilar species, *L. brachyantha*, which is uncommon and restricted, and *L. dasyantha*, more common and widely distributed, occur in central Mexico (Figure 25). Two other species, *L. sylvatica*

and *L. virgata*, occur in northwestern South America, are about equally common, and replace one another geographically with very little or no overlap in distribution (Figure 27). There is rather close, although possibly coincidental, similarity between *L. dasyantha* and *L. virgata*.

SECTION HEMISPADON

The flowers in this section have very strongly dimorphic stamens (Figure 8). The lower pair are longer, with broad connectives and thickened filaments. Their anthers are large, shaggy pubescent, connivent, short mucronate, and at least partially visible beneath the upper lip of the corolla. The upper pair of stamens are short, sterile, and filiform. Infrequently there are deformed anthers of one or two unequal locules on these short filaments which rarely contain a small amount of pollen. The corollas are red, very exceptionally pale orange or pink. The tubes tend to be more nearly cylindrical, indistinctly or not ventricose, and often slightly narrowed at the mouth (Figures 28, 34). Instead of a gaping mouth where the lips become separated, the proportionately long and narrow lips tend to continue the line of the tube. The relatively long, parallel portions of the two lips are an inconspicuous but regular characteristic of this section with the single exception of *L. jaliscana*. The upper lip shelters the mouth and the two large, mucronate anthers. The small palate is displayed some distance from the true mouth, usually as a slight construction at the base of the short lobes of the lower lip. These species have relatively uniform flowers which at best could be separated into groups with slightly broader and narrower corollas. The leaves are of two general kinds, those which are sessile and truncated to cordate basally, and those which are tapered to the base, thus appearing as though petiolate.

The distribution of vegetative characters in section *Hemispadon* is shown in Figure 11. Line 1 separates the species with sessile, mostly cordate and clasping leaves from those below the line which appear as though petiolate, having blades tapered or rounded to the base. Line 2 separates the species which tend to be heavily pubescent and mostly glandular from those below the line which mostly are glabrate or glabrous and not glandular. The leaves, stems, and calyx of species 3, *L. gutierrezii*, are densely scabrous

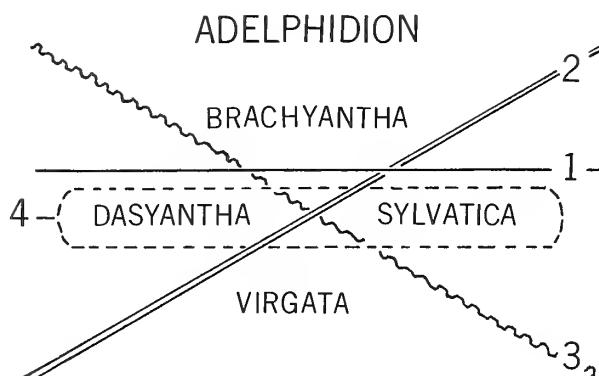


FIGURE 10.—Approximate systematic position of species in section *Adelphidion* showing distribution of taxonomic characters. Above line 1 the leaves are sessile, cordate, deltoid, and glandular pubescent; the calyx always is serrate, glandular pubescent; and the corolla always is strongly galeate. Below line 1 the leaves are tapered or rounded to a petiole-like base, and mostly glabrous and nonglandular; the calyx is variable; the corolla is little or not galeate. Above line 2 the species occur in central Mexico; below, in South America. To the right of line 3 the stigmas and anthers always are included; to the left, the stigmas are exerted and the larger pair of anthers usually is at least partially exposed in the mouth of the corolla; and often there are small appendages in the sinuses of the calyx lobes. Line 4 indicates the palates are well developed and more or less occlude the mouth of the corolla.

HEMISPADON

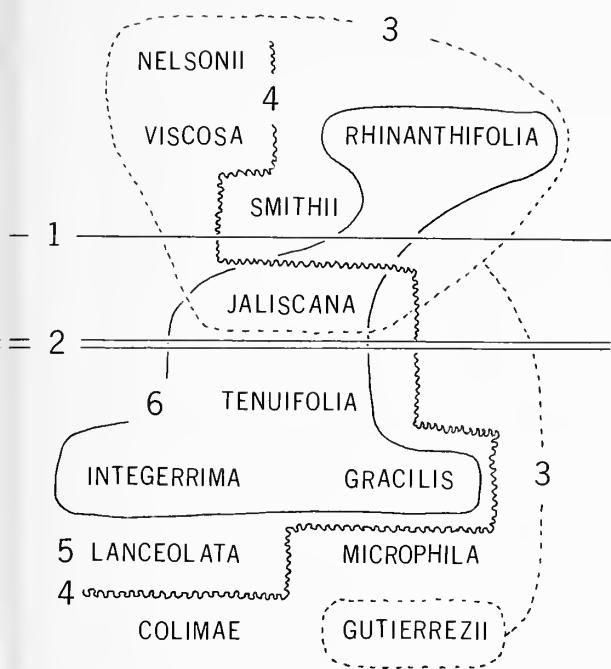


FIGURE 11.—Approximate systematic position of species in section Hemispadon showing distribution of taxonomic characters. The leaves above line 1 are mostly sessile and clasping; below they are more or less petiolate and tapered or rounded to the base. The species above line 2 mostly are glandular. Line 3 indicates the species with conspicuous pubescence on leaves, stems, and calyx. To the left of line 4 the leaves mostly are lanceolate, to the right they mostly are ovate. Species 5 has dependent inflorescences, all others are erect. The species within line 6 mostly have proportionately broad corollas; outside the line they are narrower.

pubescent. This would seem to link this species to the *L. viscosa* complex; however, the plants of *L. gutierrezii* are totally devoid of glands and the leaves are petiolate, which is the reason this species is placed in the glabrous-glabrate complex near *L. lanceolata*, *L. colimae*, and *L. microphylla*. Line 4 separates the species with primarily lanceolate leaves from those mostly with ovate leaves. In this section, species 5, *L. lanceolata*, having deliquescent growth, dependent inflorescences, and resupinate flowers, is unique; however, there are three species with similar characters in section Lamourouxia. All other species in section Hemispadon have excurrent growth and ascending inflorescences. Line 6 shows those species which tend to have broader corollas in proportion to their lengths.

The two most common and most widely distributed species are *L. viscosa*, mostly with narrow corollas and glandular calyx, and *L. rhinanthalifolia*, mostly with broader corollas and nonglandular calyx (Figure 3). These species normally are quite distinctive but at times have overlapping characteristics, perhaps indicating hybridization, and they also appear to be closely allied with *L. nelsonii* and *L. smithii*, both rather rare and restricted (Figures 29, 30). Various combinations of characters mark *L. gutierrezii*, *L. jaliscana*, and *L. lanceolata* as exceptional. The last two, although clearly linked to Hemispadon, have some characters in common with section Lamourouxia. Three species, *L. gracilis*, *L. tenuifolia*, and *L. integerrima*, although not appearing very closely similar, have relatively large and broad corollas. These last three species share elongated or lanceolate leaves with *L. lanceolata*, and this last species seems to intergrade with *L. integerrima* in Guatemala. Although there are strong differences in the leaves, *L. lanceolata*, *L. colimae*, *L. gutierrezii*, and *L. microphylla* tend to have similar, relatively narrow corollas.

Eight species occur only in Mexico north of the Isthmus of Tehuantepec; *L. lanceolata* and *L. viscosa* cross this Isthmus; *L. integerrima* and *L. gutierrezii* are restricted to Central America (Figure 3).

Floral Function and Pollination

Floral morphology exhibits a myriad of subtle to conspicuous variations, for example, in the degree of lobing of the lips of the corollas (Figure 12) and whether or how the lobes are reflexed. The abundance of these minor variations among and especially within species negates their value for taxonomic purposes and also suggests that they are of little or no evolutionary significance. Characters of the calyx, like some vegetative characters, such as shape and marginal incisions of the leaves or lengths of petiole, sometimes are helpful taxonomically but probably also are of little or neutral selective value. Those floral characters directly involved in the process of pollination, on the other hand, such as color of the corolla and development of the stamens provide the criteria for clustering the species into sections and reaffirm the observation that the process of pollination gives meaning to floral morphology (Straw, 1956; Thompson & Ernst, 1967; see also Carlquist, 1970). The most important taxonomic characters in *Lamourouxia* also

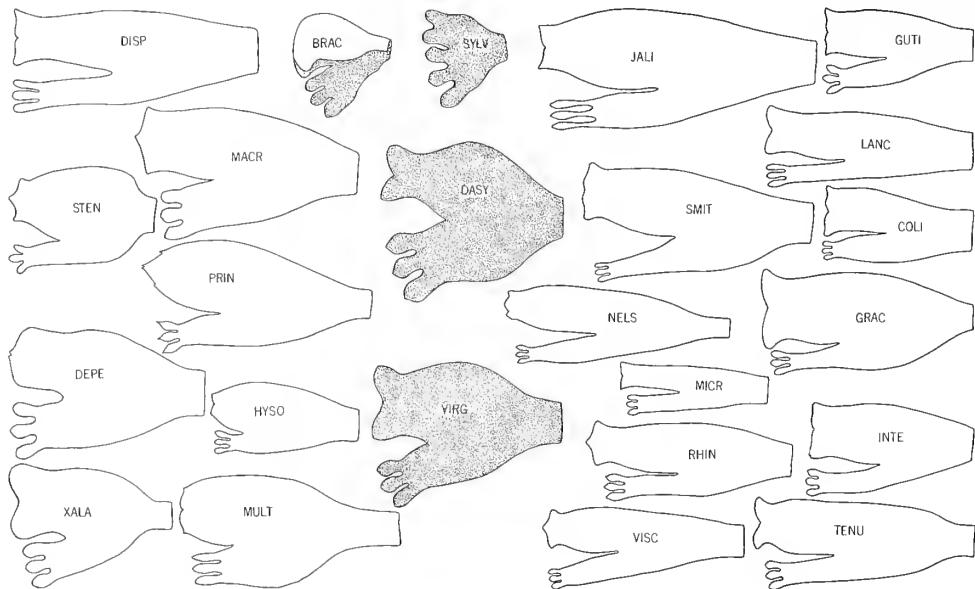


FIGURE 12.—Sample diagrams of opened corollas of *Lamourouxia* comparing characters of the upper and lower lips which are considered to be of relatively low selective value, section *Lamourouxia* to the left (omitting *L. ovata* and *L. parayana*), section *Adelphidion* central and stippled (*L. brachyantha* shown folded because it is so strongly galeate), section *Hemispadon* to the right.

are biologically significant.

The corollas are bilabiate, horizontal or inclined, bilaterally symmetrical tubes. The lips are dissimilar and somewhat different from species to species (Figure 12); however, the upper lip tends to shelter both the mouth and the anthers in most species. The corolla tapers to a narrow cylinder around the ovary and the staminal filaments are inserted at the same level on the corolla within a few millimeters of its base. At their insertion the filaments are thickened, geniculate, frequently densely pubescent, and probably secretory. The corolla wall at the insertion of the stamens frequently is pubescent. The base of the ovary sometimes also appears as though secretory. The young ovary more or less is blocked off from the corolla chamber by the hairs and swollen bases of the filaments. The deformed or ventricose corollas and the secretorylike bases of the filaments suggest mechanisms for presenting nectar. The palate on the lower lip is centrally creased with a groove that leads deep into the corolla chamber toward the nectar.

The stigma is above and beyond the anthers and pointed downward by the curved style; both are spatially removed from the ovary and nectariferous region by the length of the elongated corolla, and by

the elongated filiform, style, and filaments. The stigma and anthers are near the roof or above the mouth of the corolla. The downward direction of the stigma, the downward restriction of the movement of the pollen, the overhanging upper lip of the corolla, and the recessed or smaller lower lip, suggests that visitors arrive straight on or on the rise from below. The dorsal portion of the visitor's body would automatically contact the stigma first and then the anthers.

The structure of the flowers would appear to separate the anthers from the stigma in such a way as to favor out-crossing over automatic self-pollination. In a few specimens the anthers seem to touch the stigma, providing an opportunity for selfing, but this may be an artifact of pressing or the flowers may have been immature. Another opportunity for selfing occurs as the corollas abscise and slip along the persistent style, carrying along the epipetalous stamens so that the anthers would seem to rub against the stigma. Whether this is significant, of course, depends upon compatibility relationships and the period of receptivity of the stigmas. The corollas appear to adjust the flowers to specific pollinators and to regulate the amount of inbreeding and outbreeding (Thompson & Ernst, 1967).

THE RED COROLLAS IN MEXICO AND CENTRAL
AMERICA—SECTIONS LAMOUROUXIA AND HEMISPADON

The position of the stigma and the anthers distally and near or beyond the mouth of the corolla removes pollen as a potential lure from deep within the red corollas. That pollen probably is not the primary attraction is emphasized by the retention of the presumed secretory bases of the short, sterile filaments in section Hemispadon even though their anthers have been lost. The narrow corolla mouth, the relatively large anthers, their fixed position, shaggy pubescence, and often formidable mucros, along with the cobwebby interior of the corollas would seem especially well suited for the purposes of hovering visitors intent upon gathering nectar by means of a long, thin proboscis. The same characters would seem to discourage bodily entry into the corolla chamber by larger insects. A larger organism, such as a bumble bee, grappling with the distal portion of the corolla, as in gathering pollen, probably would be tipped off; nevertheless, there would be a good chance for such a visitor to brush against the stigma as well as the stamens. Insects small enough to enter these corollas for nectar, pollen, or shelter probably would not automatically contact the stigmas.

The literature and relevant topics concerning hummingbird pollination have been reviewed so thoroughly by Grant & Grant (1968), that one can assume, almost axiomatically, that tubular, red, scentless, nectariferous flowers, at least in the southwestern United States, are pollinated by hummingbirds. These authors have documented hummingbird pollination in 42 species representing 19 families (Grant & Grant, 1970), and predict that the total number of hummingbird-pollinated species in western North America will exceed 129 species. The red corollas of sections Lamourouxia and Hemispadon, by extrapolation, also present the syndrome of ornithophily. One of the factors substantiating this hypothesis is that bees are insensitive to red while red has been suggested to be the color most visible to vertebrates (see Sprague, p. 197, 1962). Close examination probably will show that in many cases in *Lamourouxia* the net effect is a vivid red or red-orange corolla with the mouth or tube being yellowish or orange while the abundant pubescence is dark red. Hummingbirds are assumed to occur throughout the range of *Lamourouxia*, but only one published account links *Lamourouxia* to hummingbirds (Wagner, 1946); however, other obser-

vations have been brought to my attention. Near Tepic, Nayarit, Dr. D. E. Breedlove (unpublished) observed three species of hummingbirds, the Berylline (*Amazilia beryllina*), the White-eared (*Hylocharis leucotis*), and the Rufous (*Selasphorus rufus*) visiting a variety of plants without much discrimination, among them *L. multifida* (section Lamourouxia) and *L. viscosa* (section Hemispadon). There would seem no reason to doubt that the red corollas of *Lamourouxia* are pollinated by hummingbirds.

Among the red corollas the broader, open-mouthed *L. xalapensis* (Figure 8) and the few species closest to it in section Lamourouxia (Figures 9, 21) provide a strong contrast to the narrow-mouthed corollas of the remainder of section Lamourouxia and all of section Hemispadon. The open-mouthed corollas have exserted stigma, exserted and spreading anthers, and undoubtedly freely admit smaller insects into the corolla chamber. The exserted anthers would seem to place the pollen beyond the reach of any small insects sheltering in the corolla chamber, and there are few or no glandular hairs surrounding the corolla mouth. These exserted anthers do not have conspicuously elongated spurs.

Wagner (1946) appropriately observed the Mexican Violet-eared hummingbird, *Coulibri t. thallassinus*, with pollen-dusted heads, visiting the flowers of *L. xalapensis* ("*L. exserta*") in the mountains surrounding the Valley of Mexico. He believed these flowers to be proterogynous, the nectar being produced only during the first few days, after which the hummingbirds were attracted by small insects sheltering in the corollas. The racemes of *L. xalapensis* are dependent, the tips pointing downward. The flowers are displayed on longer, more flexible pedicels which allow the flowers to invert to their normal dorsiventral position. Maturation of the flowers is acropetal but in a descending direction. Thus, it would seem that the flowers on erect inflorescences may be protandrous while those on dependent inflorescences may be protogynous.

The modifications of the corolla which appear to be accommodations to certain pollinators imply a mutual dependency between pollinator and flower for stability in proportion and shape. It is, therefore, surprising that variation in lengths of corollas in four species with red corollas can have extremes differing by a factor of at least two. These extremes for corolla length in section Lamourouxia are *L. longiflora*, 26–56 mm; *L. macrantha*, 30–60 mm; *L. multifida*, 22–55

mm; and in section Hemispadon, *L. viscosa*, 30–60 mm. This suggests that these species may be responding to different pollinators or that their pollinators are indiscriminate, pointing out the difficulty in attempting to correlate taxonomic and biologic concepts for these species.

THE NON-RED COROLLAS IN SOUTH AMERICA AND MEXICO—SECTION ADELPHIDION

The corollas of section Adelphidion collectively are shorter in length, relatively more broadly funnelform, and they suggest the syndrome of melittophily (Faegri & van der Pijl, 1966). Perhaps one of the more important reasons for this conclusion is the absence of bright red color as the corollas tend instead to be pink, lavender, or magenta, and possibly have other components which are visible to bees (see Eisner, Silberglied, et al., 1969; Macior, 1971). The corolla mouths are at the broadest portion of the tubes as in *L. xalapensis* of section Lamourouxia. The large mouths, however, are not necessarily open and tend to be obstructed by the large, pillowlike palate in *L. sylvatica*, less so in *L. dasyantha*, and partially obstructed by the large anthers and their broad filaments in *L. virgata*, open but looking downward in *L. brachyantha*. The larger pair of anthers is included within the corollas of *L. brachyantha* and *L. sylvatica*, but partially exposed beneath the upper lip in *L. dasyantha* and *L. virgata*. The smaller, upper pair of anthers mostly are fertile and bilocular, but always deeply included within the corolla chamber. If these included anthers are to have a function, the pollinators must bodily enter the corolla chamber. Macior (1971) cautions that "coadaptation between pollination mechanisms and pollinators cannot be accurately inferred on morphological grounds alone."

These corollas seem more like bee- or gullet-type flowers. There is no reason to doubt that insects other than bees or that hummingbirds also visit these flowers. Probing of these corollas by hummingbirds for nectar or for very small insects, however, would seem to require awkward or purposeful maneuvering to accomplish pollen transfer to the appropriate stigma. Very small insects entering these corolla chambers for shelter, nectar, or to gather pollen, probably would not automatically touch the stigma. These flowers probably are pollinated by beelike organisms approximately as large as the corolla mouth

so that they automatically touch the stigma and the anthers while struggling to enter the corolla chamber, perhaps each species of section Adelphidion requiring a different pollinator.

The morphology of the flowers of *L. virgata* seems somewhat ambivalent in that the corollas are longer, sometimes magenta or reddish in color, and the larger pair of anthers and their thickened filaments are displayed in the corolla mouth. These flowers would seem sufficiently similar in appearance to those of sections Lamourouxia and Hemispadon that they ought to attract hummingbirds; but, at the same time, the smaller, upper pair of anthers usually is fertile and always included, suggesting that pollinators are expected to enter the corolla chamber. In this species we may have a model to illustrate the situation suggested by Baker & Hurd (1968, p. 397) in which a flower type may be adapted to more than one kind of pollinator. Assuming that characters of the flower involved with pollination are labile, it is easy to visualize that a shift in emphasis to one or the other pollinator could lead, on the one hand, to ornithophilous flowers like those of section Hemispadon and, on the other hand, to more melittophilous flowers like the others of section Adelphidion without an "interregnum" period.

Synopsis of Vegetative Characters

Vegetative morphology exhibits a wide diversity of distinctive characters which are useful for taxonomic purposes. With few exceptions, the vegetative differences among and within species seem trivial and probably of relatively low selective value. Perhaps this is an indication that most vegetative characters are mutually efficient in this genus and that they have become variously recombined so that there no longer are whole blocks of characters to indicate distinct phylogenetic lines. This recalls a situation in the Asclepiadaceae called reticulate variation (Ehrlich & Holm, p. 258, 1963) which may be the result of complex, obligate insect pollination mechanisms in these plants. It is difficult to predict the advantage of a petiole of less than a millimeter in length over that of a sessile leaf blade. One might easily assume that photosynthetic activity is about as good in one kind of leaf shape and margin as another. If this be true, vegetative characters might be expected to be less stringently affected by the whims of selection

and to indicate important, long-standing phylogenetic relationships. Similar species with relatively many vegetative characters in common might represent rather recent or contemporary biosystematic contacts. Dissimilar species seeming to have some common vegetative similarity may represent vestiges of ancient phylogenetic alliances which no longer have any biosystematic relevance—or they might be products of random convergences. It is difficult to accept a taxonomy which places taxa with opposite floral extremes side by side merely because their leaves are similar. On face value, two plants with very similar flowers potentially seem more likely to be closely related than two plants having only similar leaves in common. Some of the vegetative characters help to support the clustering of the species within sections; however, vegetative characters alone do not appear to offer a general explanation of relationships in *Lamourouxia*.

For graphic representation of vegetative relationships 11 categories of characters were coded and compared for matching similarities. For an example of similar coding technique see Ernst, 1967. Each character exhibits from two to five contrasting states which collectively exhaust the supply of traits for distinguishing the species of *Lamourouxia* vegetatively. The characters vary in many instances beyond the limits of the coded states, necessitating value judgments as to the most representative condition for the species. Some kinds of characters, such as size of blade or length of petiole, may be similar among the leaves of some species; however, this is an abstract comparison since the texture, margin, or pubescence may be so different as to negate the association as a similarity when visually compared.

The purpose of the circular graph (Figure 13) is to show the strength of intersectional vegetative similarities among 36 independent pairs of species sharing a maximum of 8 to 10 similarities out of a total of 11 categories. The species names are arranged alphabetically around the circle and grouped by sections. Fully half the lines connect species from different sections; the scarcity of lines connecting species within sections suggests the lack of correlation between floral and vegetative characters. Adelphidion appears to have more vegetative characters in common with Hemispadon than with section Lamourouxia; this supports my argument that Hemispadon has been derived from Adelphidion. That section Lamourouxia appears to have more vegetative characters in common with Hemispadon than with Adelphidion is in

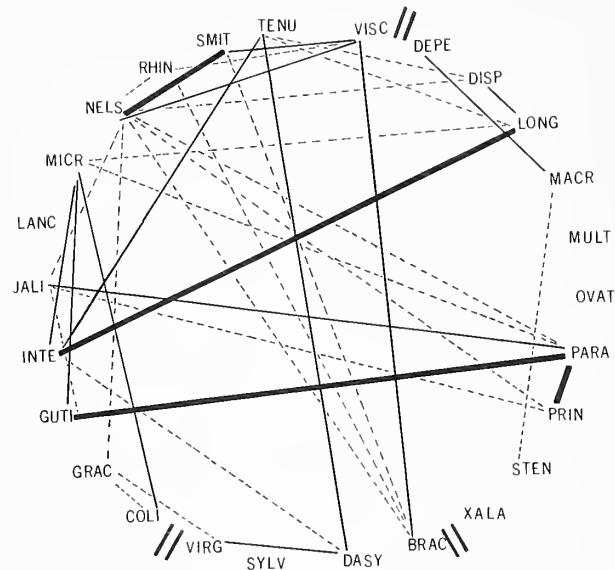


FIGURE 13.—Table comparing various strengths of intersectional vegetative similarities (explanation in text); broad line indicating 10 similarities, narrow line 9, and broken line 8; species names arranged alphabetically by section, Hemispadon to the left, Adelphidion below central, section Lamourouxia to the right.

direct contradiction of my view that sections Lamourouxia and Hemispadon have had different phylogenetic pathways. In Adelphidion, where there are the fewest species to compare, there is less internal similarity than in sections Lamourouxia and Hemispadon where there are more species to compare. The relationship between sections Lamourouxia and Hemispadon is mentioned again in the discussion.

A few of the lines on the circular graph identify close similarities among these species. The line between *L. parayana* and *L. pringlei* correctly identifies the strong similarity between these species. The intersectional lines connecting *L. brachyantha* to the arc between *L. nelsonii* and *L. viscosa* recalls to mind that Greenman (1905), disregarding floral morphology, originally placed *L. brachyantha* in Hemispadon near *L. rhinanthifolia*. If similar reasoning were to prevail, with vegetative morphology considered more important than floral, it would be just as valid to associate *L. longiflora* (Lamourouxia) with *L. integrerrima* (Hemispadon); *L. parayana* (Lamourouxia) with *L. gutierrezii* (Hemispadon); *L. dasyantha* (Adelphidion) with *L. tenuifolia* (Hemispadon); and *L. xalapensis* (Lamourouxia) with *L. lanceolata* (Hemispadon).

Discussion

SYSTEMATICS AND DIFFERENTIATION OF THE SECTIONS

Floral characters seem more useful than vegetative characters for evaluation of species relationships in *Lamourouxia*. The features of the flowers on which the sections are founded, as well as those demarcating species, are simple modifications in color, proportion, position, or shape which do not involve reorganization of floral vascular structure. Conformity within the sections centers on sets of characters which have functional significance in the process of pollination (see Ornduff, p. 121, 1969). While some characters of the flowers probably have relatively low selective value (Figure 12) those characters directly associated with the pollination system (Figure 8) probably are labile and have high selective value. This suggests that pollinators may have bred some corolla shapes that are deceptively similar in function or appearance from genetically rather different stocks.

Differences in color and shape of the corolla and in the development of the stamens appear to record changes in the pollination system of *Lamourouxia*. Aside from purely attracting and protective functions (see Straw, 1956), the net effect of these differences almost certainly ensures that pollen is precisely applied to and withdrawn from the bodies of the established pollinators. In this respect, the proposed arrangement of the species appears to be an inadvertent classification of the pollinators. Since the morphological reasoning for the clustering has been explained, it now is appropriate to consider what circumstances might have surrounded the differentiation of these groups as a kind of test of the systematic value of this arrangement of the species. For the purpose of this discussion, it is not so important that the pollinators are assumed to be bees and hummingbirds but, rather, that there are two distinctive floral morphologies—the one adapted to pollinators that bodily enter the corolla chamber, and the other adapted to pollinators that only insert a narrow proboscis into the corolla chamber.

In most flowers of section *Adelphidion* the pair of short stamens with smaller, deeply included anthers mostly produce pollen, suggesting that these anthers are functional in the process of pollination. The fact that these anthers are smaller and sometimes sterile or rudimentary perhaps indicates that they are of secondary importance. One presumes, however, there

must be some selective advantage to their continuing presence or they surely would be lost as in section *Hemispadon* (see discussion of staminode in *Pentstemon*, Straw, p. 117, 1956). The equivalent pair of short, deeply included stamens in *Hemispadon* mostly have sterile or rudimentary anthers but, in a few flowers, these anthers produce a little pollen, suggesting their potential for full restoration were there a sustained function for this pollen. Pollinators, it may be inferred, bodily enter the corolla chamber and contact the small stamens in *Adelphidion*, but in *Hemispadon* pollinators hover outside, inserting only a narrow proboscis into the corolla chamber and do not contact the small, sterile or rudimentary anthers. This suggests that anthers, having lost their role in reproduction, cease to produce pollen and become rudimentary.

Not only do the stamens provide the means for separating the species into plausible sections, they also illustrate a natural morphological sequence (Figure 14) showing the upper pair of anthers in full development in section *Lamourouxia*, in an intermediate condition in *Adelphidion*, and reduced to sterile rudiments in *Hemispadon*. This open-ended sequence can be read in either direction and, theoretically, is reversible from the morphological point of view. The possibility of morphological reversals seldom has been acknowledged (see Eyde, 1971). Other reversible and irreversible situations were mentioned by Carlquist (1970). In potentially reversible sequences it is difficult to arrive at a clear understanding of primitive

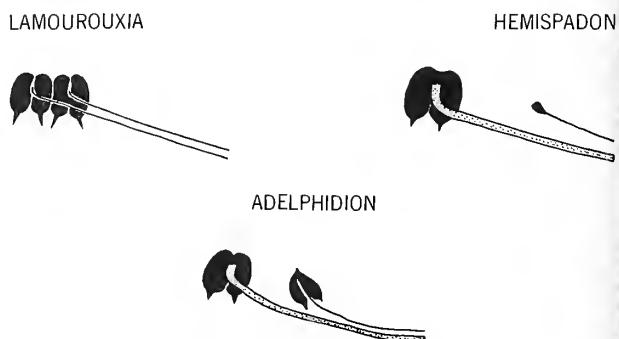


FIGURE 14.—Diagrams comparing staminal development in the three sections of *Lamourouxia*, only one of each pair of stamens shown. Left, two pairs of fully developed anthers, the filaments subequal; center, one pair of large anthers, one pair of smaller anthers; right, one pair of fertile anthers, one pair of sterile filaments.

conditions. In *Lamourouxia* the pollination syndrome and the evolution of the stamens appear to be inseparable. This provides an opportunity to consider change from one morphological state to another as change from one selection regime to another.

Color and shape of the corolla are presumed relatively labile from generation to generation. Within the flexibility of the genotype, this lability probably assures the continued efficiency of the flowers in regard to pollination. The readiness with which these changes may be effected can be realized from the simple nature of the extremes. The extremes for color range from red to not red; for shape the extremes range from permitting the pollinator to enter bodily into the corolla chambers to only allowing the insertion of a narrow proboscis. The stamens, by comparison, seem more complicated and are assumed to be somewhat less labile than the corolla because, in addition to the primary necessity of pollen and nectar, the anthers must be accurately placed, correctly shaped, and chronologically coordinated for meiosis and anthesis with the remainder of the flowers. Anthers having no purpose, as suggested by the flowers of *Hemispadon*, are lost, probably by default.

The ornithophilous flowers of section *Lamourouxia* and of section *Hemispadon*, and the melittophilous flowers of *L. brachyantha* and *L. sylvatica* (section *Adelphidion*) appear to be too strongly committed to their adaptive modifications to their respective pollinators to be readily susceptible to major modifications. As long as the established pollination regime does not change, the floral morphology in these taxa will remain relatively stable. The kinds of flowers most pliable to change probably are sufficiently flexible to be pollinated by more than one kind of visitor as suggested by Baker & Hurd (p. 397, 1968). The morphology of *L. virgata*, section *Adelphidion*, suggests that this species may be pollinated by bees as well as by birds. The color of these corollas, although usually reported to be pink or rose, sometimes varies to magenta or red. The larger anthers and their long filaments are partially exposed in the corolla mouth; the smaller included anthers usually are fertile but sometimes they are rudimentary or sterile. The mouth is relatively open and the palate is only moderate in size. The general appearance as well as some technical characters cause *L. virgata* to resemble section *Hemispadon*.

There is no particularly urgent reason to conclude

that *L. virgata* is an ancestor of section *Hemispadon* but this species does seem like a useful evolutionary model for the purpose of illustrating how section *Hemispadon* may have been derived. Assuming that a population of *L. virgata* were pollinated both by bees and by hummingbirds, a change in emphasis of pollinators probably would have a disruptive effect on floral morphology. A surge in the frequency of visits by one kind of pollinator, as there are no intermediates between bees and birds, probably would provide an opportunity for the flowers to become better adjusted to the more frequent kind of pollinator. Natural selection would lead to flowers more conspicuously adapted to their pollinators than were their more ambivalent predecessors. Stability in the major characters of floral morphology presumes stability in the pollination regime. On the basis of these generalizations we may now consider how differences in floral morphology exhibited by the sections might be correlated with changes in the pollination regimes.

SECTIONS LAMOUROUXIA AND HEMISPADON

The red corollas of section *Lamourouxia*, with two pairs of fully developed anthers, and the red corollas of *Hemispadon*, with only one pair of fertile anthers (Figure 8), are sufficiently similar in appearance and function that one would assume them to have shared much of the same phylogenetic pathway. The sterile filaments of *Hemispadon*, our only clear landmark, must be derived but it is improbable that *Hemispadon* could have been derived directly from section *Lamourouxia* because no selective advantage can be visualized to account for the loss of a pair of anthers between functionally identical ornithophilous flowers. The rudimentary stamens in *Hemispadon*, although mostly sterile, nevertheless, are potentially functional since, from time to time, they bear small, one- or two-locular anthers with a little pollen. Their permanent decline and the continuing differences between *Hemispadon* and section *Lamourouxia* rest upon the stability of the pollination system and the unlikely occurrence of a pollinator capable of restoring these rudimentary anthers to full service.

SECTIONS ADELPHIDION AND HEMISPADON

Derivation of *Hemispadon* from *Adelphidion* (Figures 8, 14) seems more likely and can be explained as the consequence of differentially labile floral organs

and a relatively sudden reversal in an established selection regime, such as ornithophilous capture of dominance in a previously ambivalent pollination system. Such a shift in emphasis of pollinators would favor redder, longer, narrower corollas. The pace of the change of the corollas probably exceeded the ability of the smaller, upper pair of stamens to adjust. The included anthers of the upper stamens became isolated from bees through elongation of the corollas and narrowing of the corolla mouths. Once their pollen was no longer involved in pollination these anthers became sterile rudiments. The filaments probably continue to exist because of their nectariferous contributions.

Difference in number of floral organs, particularly organs of the reproductive system, often delimit major groups of flowering plants. The adaptive significance of change from one number to another is difficult to appreciate by comparing families or genera (see Cronquist, p. 118, 1968) because these taxa are too remote from the circumstances surrounding the change and the transitional stages are lost or not recognized. Ultimately, such changes must be traced to the effects of selective forces operating among closely related individuals within populations. The stamens in *Lamourouxia* provide an opportunity to examine intermediate stages in a morphological series. The normally fertile, upper pair of stamens in *Adelphidion* sometimes is sterile; the normally sterile, upper pair of stamens in *Hemispadon* sometimes is fertile. This provides insight into how pollinators acting as selective forces on potentially variable, closely related plants, might have initiated the change from two pairs of fertile anthers in *Adelphidion* to one pair of fertile anthers in *Hemispadon*.

SECTIONS LAMOUROUXIA AND ADELPHIDION

Early specialization in this genus is assumed to have led, on the one hand, to flowers like those of section *Lamourouxia* favoring bird pollination and, on the other hand, to flowers like those of *Adelphidion* favoring bee pollination (Figures 8, 14). The morphological separation of these sections probably represents a prior differentiation in selection regimes than the one involving *Hemispadon* because a switch from melittophilous to ornithophilous dominance of pollination in flowers like those of *Adelphidion* is predicted to have led to flowers like those of *Hemispadon*.

The nearness of these relationships could be tested by cytological analyses of interspecific hybrids.

Within section *Lamourouxia* there are two lines of development: one with dependent inflorescence, open-mouthed, protogynous corollas, and exserted spreading stamens as in *L. xalapensis*; and the other with ascending inflorescences, more closed-mouthed, protandrous corollas, and mutually connivent anthers as in *L. multifida* (Figure 8). The flowers of *L. ovata* and *L. macrantha*, two species more or less central located in section *Lamourouxia*, are phenotypically similar and are suggestive of evolutionary modes showing how the above extremes in section *Lamourouxia* may have been derived. The inflorescences are erect in *L. macrantha* but dependent in the very similar *L. ovata*.

The depressed inflorescences in three species of section *Lamourouxia* and the same character in *lanceolata* of *Hemispadon* may be a coincidental convergence, or may be a clue to an extinction in section *Adelphidion*. If sections *Lamourouxia* and *Adelphidion* were derived from similar ancestors while *Hemispadon* was derived from *Adelphidion*, the genes for depressed inflorescence may have passed to *Hemispadon* through a now extinct species having the characteristics of *Adelphidion* (Figure 15).

Synopsis and Conclusions

Only a few floral characters are useful for appraising systematic relationships within *Lamourouxia* and the

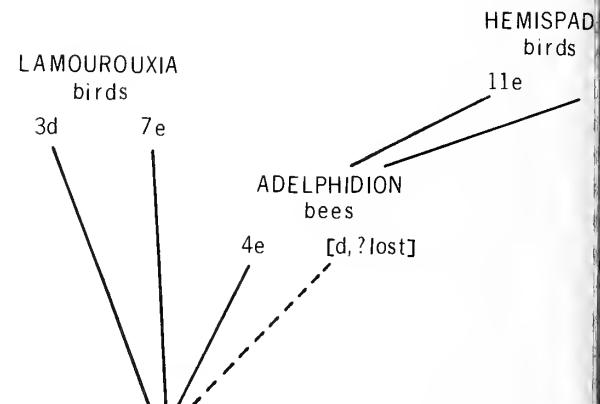


FIGURE 15.—Evolutionary implications based upon the main morphological characters of the flowers and the inflorescences for the three sections of *Lamourouxia*. The number of species with dependent (d) and erect (e) inflorescences indicated.

e concluded to have high selective value. In addition to the characters which are common to all species of the genus, conformity within the sections rests upon three criteria which are functionally correlated with the pollination system: color and shape of the corolla and the morphology of the stamens. Were it not for the stamens, the species would separate into two groups representing different selection regimes, the red-flowered, ornithophilous species, and the non-red, melittophilous species. Disparate development of the stamens, however, proclaims a more complicated evolutionary history for the red-flowered species, as some have four fertile anthers and others only have two fertile anthers. The major differences in floral morphology among the sections are attributed to changes in the pollination regimes.

The somewhat scattered distribution of vegetative similarities suggests that the characters of the ancient species may have become recombined through some kind of reticulate pattern of evolution so that phylogenetic significance is obscured. Those instances where floral and vegetative morphology seem to be correlated might be examples of random convergences or examples of more recent or secondary speciations. Lack of recognizable patterns in geographical distributions corresponding to patterns in floral or vegetative morphology returns us to the proposition that pollinators may have bred some flowers that are deceptively similar from genetically rather different stocks.

Comparative floral morphology, particularly of the stamens, shows the relationship of the sections to be Lamourouxia — Adelphidion — Hemispadon, and by implication, these plants are, respectively, bird—bee—bird, in regard to pollination. The only cytological information available is one diploid count for section Lamourouxia (*L. longiflora*, $n=7$) and one tetraploid count for Hemispadon (*L. viscosa*, $n=14$). In general, this sequence appears to read from left to right (Figures 8, 14). Since the characters of the corolla directly involved in the process of pollination are concluded to be labile, there is no reason why this morphological sequence, given the appropriate pollinators and circumstances, could not proceed in either direction or reverse itself. Most of the present species, however, suggest states of terminal specializations for their respective pollinators and for these, a major reversal of the pollination system probably would have to overcome an enormous amount of inertia.

The flowers of *L. virgata*, section Adelphidion, are

singled out as being less specialized and perhaps pollinated by bees as well as by birds. This species is used as an example to show how a change in the regular pollination regime could lead, on the one hand, to flowers like those of section Hemispadon and, on the other hand, to flowers more specialized for bee pollination. Although section Hemispadon and section Lamourouxia are superficially similar, comparative morphology of the stamens suggests that Hemispadon is derived from Adelphidion. The differences between sections Lamourouxia and Adelphidion are attributed to a similar but earlier differentiation in the pollination regimes.

Some authors (see Percival, p. 117, p. 154, 1965) have observed that the foraging behavior of bees and of at least one species of Old World Sun-birds tends to be from bottom to top in protandrous, racemose inflorescences. If generally true, this would favor out-crossing of the lower, older flowers. Proterogyny in dependent, racemose inflorescences, such as those of *L. ovata*, *L. dependens*, and *L. xalapensis*, therefore, might be a compensation to facilitate out-crossing of the lower, younger flowers. One might easily surmise from observing hummingbird behavior that these organisms are much too ingenious to restrict their foraging activities to so narrow a pattern as that characteristic of bees. Among others, Baker & Hurd (1968, p. 394) and Grant & Grant (1968, 1970) suggest that bee pollination existed before bird pollination. The differences in the inflorescences of section Lamourouxia perhaps represent ancient adaptations to the foraging behavior of bees that predate ornithophily in this genus.

The foregoing discussion explains, primarily on the basis of comparative morphology of the flowers, the objectivity of clustering the species of *Lamourouxia* into and within sections. The nature and distribution of the floral characters in this arrangement of the species suggests that adaptations to hummingbird pollination are superimposed on earlier adaptations to bee pollination. This provides insight into the evolution and survival value of the sets of characters which distinguish the sections and implies that stability in floral morphology, hence conformity within the sections, depends upon natural selection and stability in the pollination regime. From this position, we may rationalize that the evolutionary units of importance are the local, interbreeding populations where the principal selection regime is the pollination

regime. A disruption of the established selection regime, such as switch from bee to bird, or a change in emphasis from bee *and* bird to bee *or* bird pollination, probably would initiate differential reproduction of genotypes and provide the impetus for the changes in floral characters which distinguish the sections of *Lamourouxia*. This interpretation appears to strengthen support for the proposed arrangement of the species and for the taxonomic conclusions expressed in this paper; however, it also confronts us with a morphological series which, depending upon the circumstances of natural selection, might proceed in either direction, and the phylogenetic dilemma that the sections of *Lamourouxia*, and perhaps also some of the species, at least in part, might represent the independent products of convergent evolution.

Taxonomy, Key, and Descriptions

Lamourouxia H.B.K., Nov. Gen. 2: ed. folio 269, ed. quarto 335. "1817," 1818. Nom. cons.

Plants herbaceous, perennial, and probably hemiparasitic, the leafy stems somewhat woody below, from a gnarled burl; stems excurrent and ascending, or deliquescent and/or arching over other vegetation. Stems, leaves, and calyces pubescent, sometimes glandular, or glabrous; corolla always pubescent, sometimes glandular. Hairs uniseriate, sometimes terminated by a gland; branched hairs mostly confined to the corolla, often mixed with simple hairs. Leaves and floral bracts similar, opposite throughout, sessile to petiolate, pinnately veined, craspedodromus, margins sometimes entire but mostly incised, the secondary veins usually terminating at the sinus. Flowers many, pedicelled and solitary in axiles of frequently foliaceous bracts;

bracteoles absent. Inflorescences terminal, racemos simple or branched from below. Calyx tubular or panulate, four-lobed, often somewhat bilabiate, persistent. Corolla tubular, elongated, pentamerous, bilabiate, the larger upper lip morphologically two-lobed, although often appearing as one, strong galeate in bud, but inverted naviculiform or mostly little or obscurely galeate after anthesis; the dissimilar lower lip three-lobed and partially enclosing upper lip before anthesis. The corolla with the epipetalous stamens deciduous. Stamens diadelphous, insert near base of corolla, but one pair above, one below as the flowers are ascending or horizontal; stamens homoeomorphous or dimorphous, the upper pair shorter and sometimes with vestigial or smaller anthers; fully fertile anthers two-locular at maturity mostly shaggy pubescent, frequently connivent, mostly sheltered by the upper lip of corolla, or exserted and spreading. Locules of fully fertile anthers more or less equal, laterally dehiscent, nonconfluent, often mucronate basally. Pollen tricolpate. Ovary bilocular, style narrowly attenuate, stigma more or less two-lobed, mostly exceeding anthers and usually exserted. Ovules numerous, multiseriate, radially inserted on two axile placentae. Capsules mostly ovoid, apically attenuated into crooked base of style, loculicidal from above. Seeds small, tightly packed, about twice as long as wide, truncated, sides somewhat angular, with uniform, polygonal reticulations. Dicotyledoneous embryo orthotropous, contained in a small envelope of endosperm (Figures 1, 6, 8).

LECTOTYPE SPECIES.—*L. multifida* H.B.K. (Taxon 18: 480. 1969).

DISTRIBUTION.—Twenty-four species, from northern Mexico to western Panama, and two species, Colombia to central Peru (Figure 2).

Key to *Lamourouxia*

1. Stamens subequal, the 4 anthers more or less equal in size, fertile, mutually connivent near the mouth of the corolla or exserted and spreading; corolla red I. SECTION LAMOUROUXIA
Species 1–10

I. SECTION LAMOUROUXIA

Species 1–10

2. Plants upright, excurrent, branches ascending at acute angle, inflorescence tips ascending.
3. Leaves 1- or 2-pinnately, deeply, and narrowly divided; widespread, Mexico and Guatemala 1. *L. multifida*
3. Leaves not divided.
4. Leaves lanceolate or oblanceolate; length 3× (or more) width.

Key to *Lamourouxia*—continuedI. SECTION LAMOUROUXIA—continued
Species 1–10—continued

5. Petioles less than 1 mm long; blades tapered to base, margins \mp entire; calyx lobes subulate, 1 mm or less wide; infrequent, Chihuahua, Durango, and Jalisco
2. *L. longiflora*

5. Petioles 1–2 mm long, margins incised; calyx lobes triangular, 3 mm or more wide.

6. Base of blade acute, margins evenly dentate-serrate; Guerrero 5. *L. dispar*

6. Base of blade obtuse to truncate, margins irregularly doubly dentate-serrate-crenate; Chiapas (?Guatemala) 7. *L. stenoglossa*

4. Leaves ovate to obovate or length 3 \times (or less) width.

7. Leaves elliptical to obovate, 9 mm or less wide, rounded or tapered to base, petioles 1 mm or less long.

8. Blades membranous, ovate, evenly crenate, sparsely pubescent; calyx 5–6 mm long; southwestern State of Mexico 3. *L. parayana*

8. Blades coriaceous, elliptical, obovate to spatulate, margins entire to irregularly few-dentate or -crenate, densely scabrous pubescent; calyx 9–10 mm long; Hidalgo, Oaxaca 4. *L. pringlei*

7. Leaves broadly ovate, cordate, 15 mm or more wide; margins irregularly, doubly, multi-serrate-dentate-crenate, petioles 2–8 mm long; Mexico (?Guatemala) 6. *L. macrantha*

2. Plants dependent, deliquescent, branching frequently at nearly right angles, inflorescence tips arching downward, flowers resupinate.

9. Leaves sessile, ovate, cordate, 22–37 mm wide; Oaxaca 8. *L. ovata*

9. Leaves with petioles 1–7 mm long, blade 6–23 mm wide.

10. Leaves ovate, calyx and leaves mostly pubescent (sometimes glabrous), axil of sinus of calyx revolute, protruding; Guatemala 9. *L. dependens*

10. Leaves lanceolate, calyx and leaves mostly glabrous or glabrate; Mexico, north of Isthmus of Tehuantepec 10. *L. xalapensis*

1. Stamens strongly unequal, the anthers dimorphic, the longer pair of filaments thickened, their anthers large, usually connivent near the mouth of the corolla or barely exposed; the shorter pair of filaments filiform, their anthers smaller, rudimentary, or absent, always deeply included.

11. Fertile anthers 4, the smaller pair rarely sterile; corolla lavender, pink, or magenta, not red II. SECTION ADELPHIDION
Species 11–14

II. SECTION ADELPHIDION

Species 11–14

12. Plants from Mexico.

13. Leaves ovate, cordate, glandular pubescent 11. *L. brachyantha*

13. Leaves lanceolate to subulate, tapered to base, glabrous, not glandular
12. *L. dasyantha*

12. Plants from South America.

14. Corollas 13–24 mm. long, mouth occluded by palate, anthers included
13. *L. sylvatica*

14. Corollas 29–45 mm long, mouth open, lower pair of anthers exposed
14. *L. virgata*

11. Fertile anthers 2, the rudimentary pair rarely fertile; corolla red

III. SECTION HEMISPADON
Species 15–26

III. SECTION HEMISPADON

Species 15–26

15. Calyx and leaves definitely pubescent, sometimes glandular.

16. Leaves sessile, rounded, truncate, or cordate at base.

17. Calyx glandular; average corolla 6–7 mm wide; leaves ovate to lanceolate.

Key to *Lamourouxia*—continued

III. SECTION HEMISPADON—continued

Species 15–26—continued

18. Leaves to 15 mm wide, young and old glandular-pubescent, not scabrous, margins to 14 dentate on a side, not reticulate below, calyx lobes 4–27 mm long. Infrequent, south-central Mexico 15. *L. nelsonii*
18. Leaves 15 mm or more wide, densely pubescent, often scabrous, young leaves and bracts glandular, margins 14 or more dentate on a side, reticulate venation standing out below, calyx lobes 2–4 mm long. Widespread, Mexico and Central America 16. *L. viscosa*
17. Calyx weakly or not glandular, bracts and leaves not glandular; average corolla 9–10 mm wide; leaves mostly ovate, pinnate venation standing out below.
 19. Leaves to 50 mm long, to 28 mm wide, sometimes scabrous; calyx lobes frequently irregular to dentate. Widespread in Mexico.
 17. *L. rhinanthalifolia*
 19. Leaves 50 mm or more long, 29 mm or more wide, membranous, not scabrous; calyx lobes entire; rare, Oaxaca 18. *L. smithii*
16. Leaves not sessile, tapered to the base.
 20. Leaves lanceolate, 50 mm or more long; calyx lobes 10–12 mm long, subulate, glandular; Jalisco 19. *L. jaliscana*
 20. Leaves ovate, to 25 mm long; calyx lobes 2–5 mm long, not glandular; Costa Rica and Panama 26. *L. gutierrezii*
15. Calyx and leaves glabrous or glabrate, not glandular; leaves tapered to base, neither cordate, nor sessile.
 21. Leaves ovate, elliptical to obovate.
 22. Leaves 18–28 mm long.
 23. Leaves elliptical to obovate; calyx lobes to 2 mm long, corolla 45–49 mm long, 8–10 mm wide; Guerrero, Morelos 20. *L. gracilis*
 23. Leaves ovate, calyx lobes 4–6 mm long, corolla to 35 mm long, to 7 mm wide; Colima 25. *L. colimae*
 22. Leaves less than 10 mm long; calyx lobes to 1 mm long; Oaxaca.
 21. *L. microphylla*
 21. Leaves lanceolate to subulate.
 24. Inflorescence tips ascending; calyx lobes 6 mm or less long; branching ascending.
 25. Blades subulate, irregularly dentate to 3 mm wide; Oaxaca.
 22. *L. tenuifolia*
 25. Blades lanceolate, sub-entire, 3–7 mm wide; Guatemala (?intergrading with *lanceolata*) 23. *L. integerrima*
 24. Inflorescence tips dependent; calyx lobes 6–15 mm long, spreading or reflexed; branching at nearly right angles; Oaxaca and Central America.
 24. *L. lanceolata*

I. Section Lamourouxia. Species 1–10.

Stamens subequal, the filaments similar, the 4 anthers more or less equal in size, fertile, shaggy pubescent, mutually connivent, long mucronate, near the mouth of the corolla; or exserted, spreading, less pubescent and slightly or not mucronate. Corolla red or red-orange, the tube ventricose to somewhat funneliform (Figures 8, 9, 16, 17, 21).

TYPE SPECIES.—*L. multifida* H.B.K.

DISTRIBUTION.—Ten species, Mexico and Guatemala (Figures 17, 22).

1. *L. multifida* H.B.K., Nov. Gen. 2: ed. folio 273 ed. quarto 339. "1817," 1818.

TYPE LOCALITY.—"Crescit in temperatis Nova Hispaniae inter Guanaxuato et Santa Rosa de la Sierra, alt. 1200 hex . . . Floret Septembri."

TYPE SPECIMEN.—Bonpland 4273, "Sta rosa,"

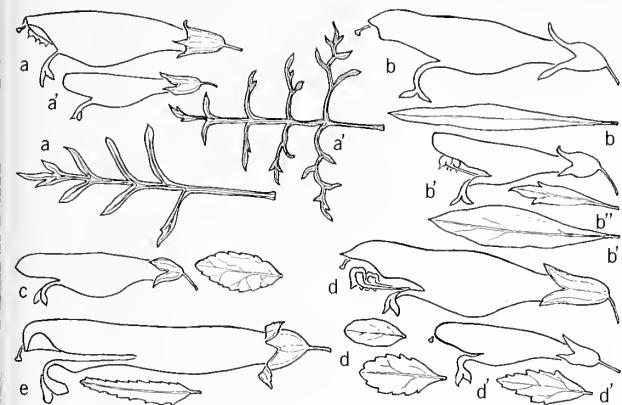


FIGURE 16.—Section Lamourouxia, diagrams of flowers and leaves. *a*, *L. multifida*, McVaugh 13437, US; *a'*, Thomas 14136, US; *b*, *L. longiflora*, Hartweg 188, W; *b'*, (*L. hyssopifolia*) Palmer 260, US; *b''*, (*L. hyssopifolia*) Goldman 210, US; *c*, *L. parayana*, Paray 2242, ENCP; *d*, *L. pringlei*, Pringle 4972, US; *d'*, Gonzales Q. 3127, ENCP; *e*, *L. dispar*, Straw & Gregory 1062, MEXU.

(in General Herbarium but not in Humboldt & Bonpland Herbarium).

SYNONYMY.—

L. laciniata Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12 (2): 32. 1845. Type locality: "Sur les basaltes de Cerro de Macuiltepeque, près Xalapa à 5,000 pieds; dans les bois de chênes et sur les rochers de Juguila del Sur (côte au sud d'Oaxaca) à 5,000 pieds . . . Mai-Septembre . . . H. Gal. no. 990." Syntype specimens: Galeotti 990, mixed data, BR (2 specimens), G, P, W.

L. laciniata var. *pilosa* Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12 (2): 34. 1845. Type locality: "Dans les bois San Pedro, près de Real del Monte, à 8,000 pieds . . . Août . . . Gal. No. 1085." Type specimen: Galeotti 1085, BR.

L. multifida H.B.K. β *grandiflora* Bentham, in DC. Prod. 10:540. 1846. Type locality: "pr. Bolanos (Hartweg! n. 187) . . . (v. s.)" Type specimens: Hartweg 187, BM, G, GH, K (Herb. Benth. "Bolaños"; Herb. Hook. "Zacatecas"), P, W.

L. grandiflora "Benth." ex. J. J. Linden, "Cat. no. 10, 6 (1855)." "Cette magnifique variété du *L. multifida* . . ." Typescript copy examined at PH; original not seen.

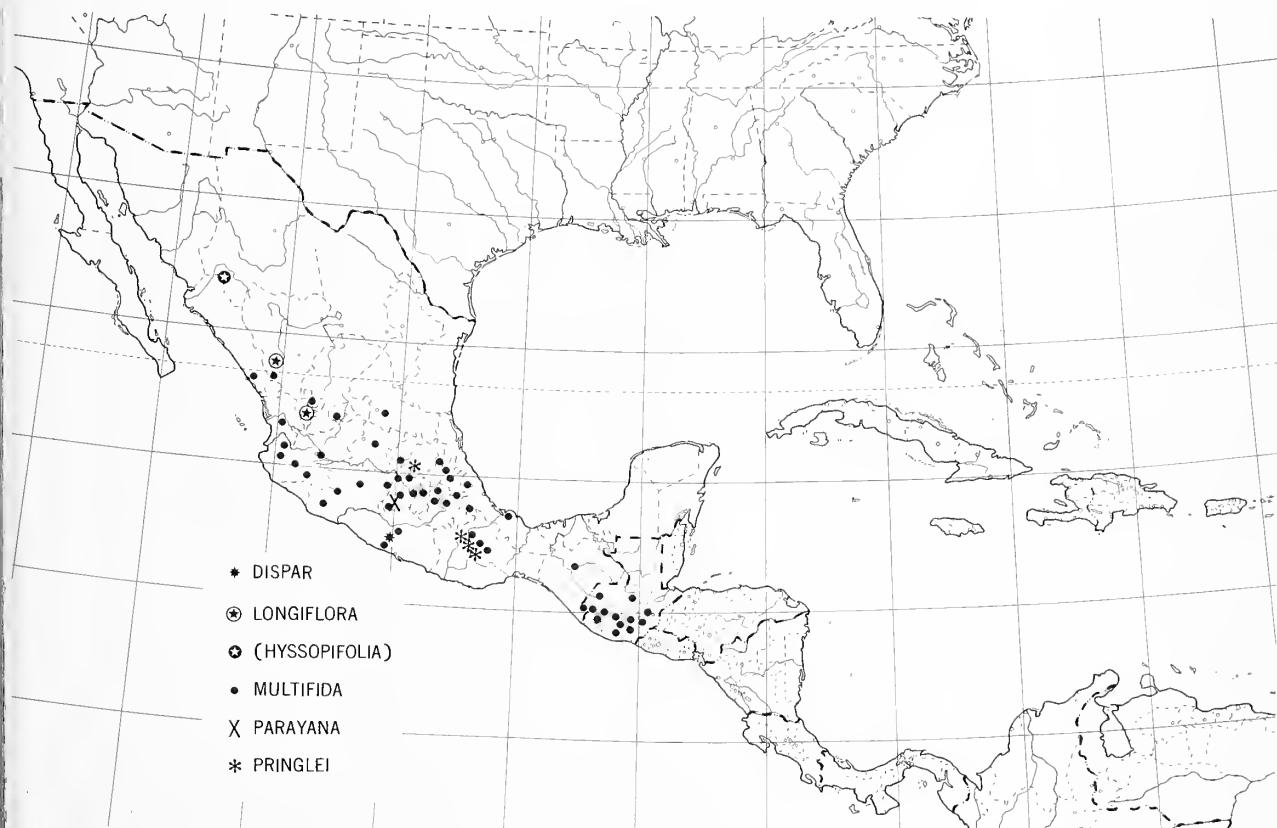


FIGURE 17.—Distribution of section Lamourouxia in Mexico and Guatemala. The position of *L. hyssopifolia* is discussed under *L. longiflora*.

L. pringlei "Gandoyer," =Gandoger, Bull. Soc. Bot. France 66:217. 1919. Type locality: "Mexico, ad. Sta Fé prope Mexico, alt. 8000 ped. (Pringle n. 7982!)." Type specimens: *Pringle* 7982, F, MO. Not *L. pringlei* Robinson & Greenman ex Pringle.

L. tepicana (M. E. Jones) Pennell in Morton, Contr. U.S. National Herb. 29: 115. 1945. Basionym: *Pedicularis tepicana* Jones, Contr. Western Bot. 15: 150. 1929. Type locality: "no. 23211, Tepic, Nayarit, February 15, 1927." Type specimen: Date mixed, *Jones* 23211, 10 Feb. 1927, POM.

Stems erect to 2 mm tall. Leaves glabrous to pubescent, 21(39)57 mm long, 10(24)33 mm broad, deeply once or twice pinnatifid, 2- to 5-lobed on a side, divisions 1-4 mm broad, mostly linear, often mucronulate, margins entire, the petiole 6(13)23 mm long, midrib standing out below. Inflorescence ascending; pedicels 2(3)6 mm long. Calyx pubescent to glabrate, 6(8)11 mm long, 4(5)7 mm broad, the lobes broadly triangular to subulate, rarely toothed, 2(4)7 mm long. Corolla red (to orange or ?pink), 22(41)55 mm long, 7(10)17 mm broad, ventricose, the upper lip 4(11)16 mm long, little or not lobed, the lobes of the lower lip 4-6 mm long. Stamens subequal, shaggy, all fertile, the anther lobes prominently mucronate below. Capsules ovoid, 9-11 mm long, 5-6 mm broad. (Figure 16). Altitude: Mexico, 800-3950 m; Guatemala, 1067-3000 m. Flowering: throughout year, peak August to December.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figures 17, 22).—MEXICO: Aguascalientes (2); Chiapas (10); Durango (*Breedlove* 1741, DS, MICH); Distrito Federal (11); Guanajuato (4); Guerrero (5); Hidalgo (7); Jalisco (12); State of Mexico (26); Michoacán (11); Morelos (*Halbinger* 78, GH); Nayarit (4); Oaxaca (10); Puebla (10); San Luis Potosí (4); Sinaloa (3); Tlaxcala (2); Veracruz (14); Zacatecas (2). GUATEMALA: Alta Verapaz (*von Tuerckheim* 2022, BR, C, F, G, GH, MO, US, W); Chimaltenango (3); Escuintla (*Eggler* 488, F); Guatemala (4); Huehuetenango (5); Jalapa (2); Quezaltenango (3); Sacatepéquez (5); San Marcos (*Steyermark* 36688, F); Santa Rosa (*Heyde & Lux* 149, G, GH, MO, US); Sololá (4); Zacapa (*Steyermark* 29796, F).

The unique, deeply pinnatifid leaves, although extremely variable, distinguish this species from all others. The subulate as well as triangular calyx lobes, and the extremes of corolla length, varying from 22-55 mm, are notable. The "var. *grandiflora*" is only one among many extremes and is an impractical

taxonomic element. This species seems closely allied to *L. longiflora*.

2. *L. longiflora* Bentham, Plantae Hartwegianae, p. 22. 1839.

TYPE.—*Hartweg* 188, unlocalized at time of publication, but later (Benth. in DC. Prod. 10: 540. 1846) identified as "in Mexico pr. Bolaños."

TYPE SPECIMENS.—BM, GH, K (Herb. Benth., "Bolaños;" Herb. Hook., "Zacatecas"), W (Figure 18).

SYNONYMY.—

L. hyssopifolia A. Gray, Proc. Amer. Acad. 21: 404. 1886. Type locality: "At the Frailes in the mountains above Batopilas, at about 7,000 feet, *Palmer*, 260." Type specimens: *Palmer* 260, GH, MEXU, NY, PH, US (Figure 18).

Stems erect, probably about 1 m tall. Leaves pubescent to glabrate, lanceolate to oblanceolate, 28-56 mm long, 3-7 mm broad, usually mucronulate apically, attenuate to base, entire or rarely 1- to 3-toothed, slightly revolute, midrib and a few laterals standing out below. Inflorescence ascending; pedicels 2-5 mm long. Calyx pubescent, 7-13 mm long, 3-5 mm broad, the lobes narrowly subulate, 2-8 mm long. Corolla red, 26-56 mm long, 6-13 mm broad, the upper lip 6-16 mm long, little or not galeate, the forward margins rounded or obtuse, usually not reflexed; the lobes of the lower lip 3-5 mm long. Stamens subequal, the anthers all fertile and shaggy, the lobes mucronate below. Capsules 7-8 mm long, 5 mm broad. (Figure 16.)

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 17).—MEXICO. Chihuahua: Near Batopilas, 5500-6500 ft, Oct. 1898, *Goldman* 210, GH, US; *Palmer* 260, Aug.-Sept. 1885 (type for *L. hyssopifolia*). Jalisco: (see type). Durango: Steep slope with *Pinus*, *Quercus*, and *Arbutus*, 46 miles north of Estacion Coyotes along a lumber road, just northwest of San Luis del Río, 7900 ft, 5 Nov. 1970, *D. E. Breedlove* 18773, CAS, US; steep slope with *Pinus*, *Quercus*, *Arbutus*, and *Juniperus*, along Highway 40, 6 miles west of La Ciudad, 8800 ft, 7 Nov. 1970, *D. E. Breedlove* 1884, CAS, US. Unlocalized: "Sierra Madre Mex. Bor." *Seemann*, BM, C, GH, K.

CHROMOSOMES. — n=7, counted by Ernst from *D. E. Breedlove* 18773 (see above).

This species is distinguished by its broad, lanceolate or oblanceolate, mostly entire leaves, subulate calyx



FIGURE 18.—Section Lamourouxia. *a*, *L. longiflora*, type collection, Hartweg 188, K; *b*, *L. hyssopifolia*, type collection, Palmer 260, GH.

lobes, and large flowers. Whether *L. hyssopifolia* is conspecific is debatable as it is known from a distant locality in Chihuahua where the dimensions of the leaves and corolla are smaller and a few of the leaves are provided with one or two conspicuous teeth. The smaller flowers from this northern locality generally resemble those of the more common *L. multifida*, a relationship that is further emphasized by the rare toothed leaves. The larger flowers of typical *L. longiflora* particularly recall the larger flowers of the type collection of *L. multifida* β *grandiflora*, Hartweg 187, also presumed to have originated from near Bolaños.

Six collections including 15 presumed duplicate specimens have been examined. If one had only a single specimen of the Hartweg collection of *L. longiflora* and only one collection of *L. hyssopifolia*, it would seem indisputable that two distinct species were represented. When all of the specimens are

viewed at one time, the range of variation is apparent and suggests that one species is a better gamble until shown otherwise by biosystematic information.

3. *L. parayana* W. R. Ernst, sp. nov.

Herba suffruticosa, perecta. Folia pubescentia, ovata vel elliptica, plus minusve crenata et scabra, brevisime petiolata. Calyx glandulopubescentia, limbis late triangularibus, acutis, mucronulatis. Corolla rubra, cylindrica, ventricosa, labio [superiore bifido, lobis] rotundatis, non vel minime reflexis; labio inferiore late trifido. Stamina omnia fertilia, subaequalia. Affinis sectionis Lamourouxia, verosimiliter *L. pringlei* sed folia ut videtur maiores et calyces parviores.

TYPE LOCALITY.—Estado de Mexico, Cerro de las Viboras, cerca de Sultepec, altitude 2500 m, 2 Nov. 1956.

HOLOTYPE.—*Ladislao Paray* 2242, ENCB (Figure 19).

Stems thin, probably erect and 1 m or less long. Leaves membranous, pubescent, slightly scabrous above, ovate or broadly elliptical, 15–20 mm long,

6–8 mm broad, crenate with 3–10 teeth on a side, narrowed to the base with a petiole of 1 mm or less; midrib standing out below, somewhat depressed above, with 2–4 faint laterals. Inflorescence ascending, the pedicels 4–6 mm long. Calyx glandular pubescent,



FIGURE 19.—Section Lamourouxia. *L. parayana*, holotype, *Paray* 2242, ENCB.

5 mm long, 5 mm broad, the lobes 3 mm long, broadly triangular, mucronulate. Corolla red, 30–37 mm long, 10–11 mm broad, ventricose in midportion of tube, upper lip 7 mm long, little or not galeate, the forward margins little or not reflexed, lobes of the lower lip 3–4 mm long, 2–3 mm broad, rounded. Stamens subequal, anthers shaggy, all fertile, the lobes strongly mucronate below. Immature capsules ovoid, 3 mm long, 5 mm broad. (Figure 16)

DISTRIBUTION.—State of Mexico, see type (Figure 7).

The flowers of this species resemble those of *L. multifida* and *L. pringlei* since the forward margins of the upper lip of the corolla are little or not reflexed and the anthers are equal in size. Unfortunately, *L. parayana* is known only from a single sheet, and without additional material, it is difficult to pinpoint the characters separating it from *L. pringlei*. The flowering stems of *L. parayana* are thin and wirelike, millimeter or less in diameter, and possibly decumbent. The dried leaves appear membranous, broadly ovate or elliptical and the nonrevolute margins are early crenate. The calyx is 6 mm or less long with the cup portion only about 3 mm deep. The flowering stems of *L. pringlei* are 2–4 mm in diameter and upright. The leaves are more coriaceous, more irregularly serrate or sometimes essentially entire, and the margins tend to be revolute or the blades are concave, varying in shape from elliptical to spatulate. The more prominent calyx is 7–12 mm long with the cup portion about 5–8 mm deep.

L. pringlei Robinson & Greenman ex Pringle, Garden and Forest 8: 273, fig. 39. 10 July 1895.

TYPE LOCALITY.—“. . . rocky and wooded summit ridges of San Felipe . . .”

TYPE SPECIMENS.—Pringle 4972, Oaxaca, “Cold edges, Sierra de San Felipe, 10,000 ft., 25 September 1894,” A, BM, BR, C, ENCB, F, G, GH, K, MEXU, FO, MSC, NY, P, PH, RSA, US, W. Not *L. pringlei* Gandoyer, =Gandoger, Bull. Soc. Bot. France 66: 17. 1919, =*L. multifida*.

Stems erect to nearly 2 m tall. Leaves pubescent, probably scabrous, the larger 13(19)24 mm long, 6(9) mm broad, elliptical to obovate or spatulate, apically rounded or acute, attenuate below, the margins serrate to crenate with up to 7 teeth on a side, entire and revolute, midrib standing out below

with 3 or 4 faint lateral veins; petiole to 1 mm long, larger leaves on major stems sometimes sessile. Inflorescence ascending; pedicels 3(4)5 mm long. Calyx glandular pubescent 7(10)12 mm long, 4(5)6 mm broad, the lobes 3(4)6 mm long, broadly triangular, entire or with 2 or 3 small teeth, the upper pair of calyx lobes separated by a shallow sinus. Corolla red or red-orange, 35(44)55 mm long, 6(10)15 mm broad, the upper lip 9(12)17 mm long, rounded to apiculate, little or not galeate, the forward margins rounded, little or not reflexed; the lobes of the lower lip 3–5 mm long, 2–3 mm broad, mostly cuspidate. Stamens subequal, all anthers fertile, shaggy, the lobes strongly mucronate at base. Capsules ovoid, 14 mm long, 7 mm broad. (Figure 16.) Altitude: 1900–3247 m. Flowering: August to January.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 17).—MEXICO: Hidalgo (6); Oaxaca (11); ?Puebla (Esperanza, *Purpus* 2796, F, GH, MO, UC, US).

The name *L. pringlei* probably was inadvertently published by Pringle in a narrative of his travels in Oaxaca in anticipation of the more formal description by Robinson & Greenman. An adequate plate with detailed enlargement of the flower and mention of the type locality by Pringle establishes the validity of this name 20 days before its publication in the revision of the genus by Robinson & Greenman, Amer. Jour. Sci. 50: 170, and, simultaneously, Contr. Gray Herb. 9: 170. 1 August 1895.

This species is quite variable with two centers of distribution within its limited range. With exceptions, the leaves of the plants in Oaxaca seem to have more rounded or elliptical leaves, and sometimes much larger corollas, while the leaves of the plants in Hidalgo tend to be more obovate or spatulate, and the margins more irregularly toothed. The proportionately large calyx and cuspidate lobes of the lower lip of the corolla are notable and help to distinguish this species from the probably closely related *L. parayana*.

5. *L. dispar* W. R. Ernst, sp. nov.

Herba suffruticosa. Folia glabriuscula, anguste elliptica vel lanceolata, serrata, attenuata basin versus. Calyx pubescens, limbis serratis. Corolla rubra, late cylindrica, labio superiore parum galeate, bifido, lobis rotundato-reflexis, labio inferiore late trifido. Stamina omnia fertilia, plus minusve subaequalia vel superiora

breviora. Affinis sectionis Lamourouxia autem corollae formam sectionis Hemispadon simulans.

TYPE LOCALITY.—Guerrero: Near Omiltemi, 20 miles west of Chilpancingo; deep pine-oak-fir cloud forest; 7500–8000 ft. Sprawling shrub to 3 ft long; corolla bright red; scarce. 31 July 1957.

HOLOTYPE.—*R. M. Straw & D. P. Gregory 1062*, MEXU (Figure 20).

ISOTYPES.—MICH, RSA.

Stems to 1 m long. Leaves variable, glabrate to sparingly pubescent, the larger 20–28 mm long, 3–8 mm broad, narrowly elliptical to lanceolate, apically attenuate, tapered to base with petiole about 1 mm long, with 5–15 serrate on a side; midrib standing out below, secondary veins faint. Inflorescence ascending, pedicels 5–6 mm long. Calyx pubescent, the major veins standing out, 8–11 mm long, 5–6 mm broad, the lobes triangular, spreading to reflexed, serrate, 5–7 mm long. Corolla red, broadly cylindrical, 55 mm long, 9–10 mm broad, little or not ventricose, rounded distally and slightly galeate, the upper lip 20–22 mm long, the lobes rounded, partly reflexed, the lobes of the lower lip 5–7 mm long, about 3 mm broad. Stamens 4, subequally developed, the upper pair shorter, the filaments thickened distally, the anthers shaggy pubescent, the lobes short acuminate basally (Figure 17).

As the name implies, *L. dispar* is enigmatic. The stamens are subequal, resembling those of the larger flowers of *L. macrantha*. The anthers are densely pubescent, relatively large, loosely or not connivent, and the upper pair of filaments is somewhat shorter than the lower, although both pairs of anthers are near the mouth of the corolla. The shape of the corolla with the lower lip continuing forward rather than arching downward recalls the morphology of section Hemispadon. The broader leaves recall some of the more dentate examples of *L. virgata* in section Adelphidion; the narrower leaves resemble those of *L. tenuifolia* in Hemispadon. The long red corollas and the four subequally developed stamens are the reasons for placing *L. dispar* in section Lamourouxia.

This species is represented by three specimens of a single collection. It appears to incorporate floral characters of section Hemispadon and section Lamourouxia. The elongated, uncrowded inflorescence with long flowers, and the long leaves suggests similar characters in *L. longiflora* as well as *L. jaliscana*. The narrow leaves of the holotype resemble those of

L. tenuifolia, while the leaves of the isotype at Michigan are more like some examples of *L. virgata*. The long, blunt corollas with their lower lip continuing forward rather than abruptly curving downward resemble those of *L. rhinanthifolia*; however, the subequally developed, fully fertile anthers place this species in section Lamourouxia.

6. *L. macrantha* Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12(2): 32. 1845.

TYPE LOCALITY.—“Aux bords des ruisseaux du Cerro San Felipe, près d’Oaxaca, de 8,000 à 9,000 pieds, et sur les versants du pic d’Orizaba, de 8,000 à 9,500 pieds . . . Août—Octobre . . . H. Gal. Nos. 94 et 1104.”

SYNTYPE SPECIMENS.—*Galeotti 994*, Oaxaca, BR G, P, W; *Galeotti 1104*, Pico de Orizaba, BR, G, W

SYNONYMY.—

L. betonicaefolia Bentham in DC. Prod. 10: 539. 1846
Type locality: “In Mexici monte Orizaba (Linden! n. 225, Galeotti! n. 944 et 1104. Ghiesbrecht!) . . . (v. i. herb. Hook. et Mus. par.)” Syntype specimens: *Linde 225*, Pico de Orizaba, BR, K; *Galeotti 944*, BR, G, P, W; *Galeotti 1104*, BR, G, W. See syntypes for *L. macrantha*.

Stems erect to 1 m tall. Leaves glabrate to pubescent, broadly ovate, basally truncate to cordate, the larger 25(50)86 mm long, 15(27)38 mm broad, appearing sessile but petioles 2–8 mm long, margin doubly serrate to dentate or crenate, the teeth to 4 mm long, rounded to mucronulate, 25–56 on a side midrib and 4–9 laterals on a side standing out below. Inflorescences ascending, pedicels 6(11)21 mm long. Calyx mostly pubescent, 11(16)26 mm long, 6(8)1 mm broad, the lobes 7(9)12 mm long, usually broad and frequently denticulate. Corolla red or red-orange (?partly yellow), 30(54)68 mm long, 10(14)18 mm broad, frequently ventricose, the upper lip 9(21)2 mm long, terminally apiculate, little or not galeate, forward margins rounded or obtuse, reflexed, the lobes of the lower lip 4–6 mm long, sometimes 5 mm broad. Stamens subequally developed, all fertile and shaggy pubescent, the upper pair sometimes with smaller anthers; mature stamens probably exserted and spreading; basal lobes of anthers barely acuminate. Capsules ovoid, about 15 mm long and 10 mm broad (Figure 21). Altitude: 2600–3500 m. Flowering August to October and January, peak August to September.

DISTRIBUTION AND NUMBER OF TYPICAL SPECIMEN

EXAMINED (Figure 22).—MEXICO: Chiapas (in pine lands, Mt. Tacaná, 2000–4038 m, Matuda 2335, GH, MICH, MEXU, PH); Durango (2); Guerrero (Cerro Teotepec, Tlacotepec, Rzedowski 18581, DS, ENCB, F, MEXU, MICH, TEX); Jalisco (2); State

of Mexico (Temascaltepec, Crucero Agua Blanca, Hinton 4926, GH, US); Oaxaca (8); Puebla (Tesmalaquilla, Balls 5335, K, UC, US); Veracruz (3). GUATEMALA: San Marcos (frequent in pine-fir-hardwood forest, San Luis west of Ixchiquán, road



FIGURE 20.—Section Lamourouxia. *L. dispar*, holotype, Straw & Gregory 1062, MEXU.

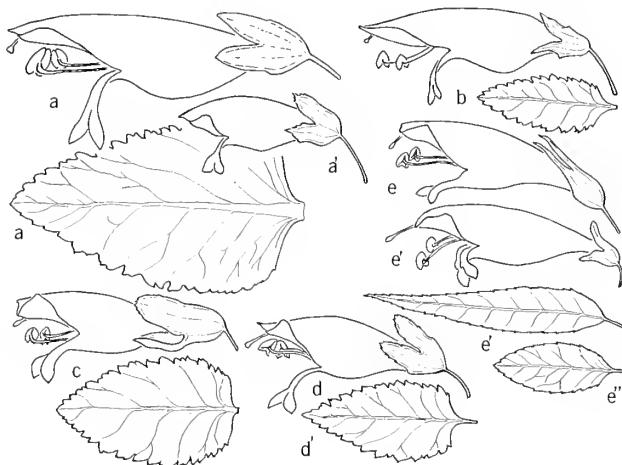


FIGURE 21.—Section Lamourouxia, diagrams of flowers and leaves. *a*, *L. macrantha*, Pringle 4854, MEXU; *a'*, Pringle 4762, PH; *b*, *L. stenoglossa*, Breedlove, 15127; *c*, *L. ovata*, Conzatti 2273, & 2294, F; *d*, *L. dependens*, Holway 568, US; *d'*, Skutch 154, PHILA; *e*, *L. xalapensis*, Pringle 8886, MSC, showing laciniate calyx; *e'*, Smith 676, US, showing regular calyx; *e''*, Hinton 11076, US.

to Tacaná, ca. 3400 m, Beaman 2342, ENCB, GH, MSC, TEX, UC, US).

DISTRIBUTION AND COLLECTIONS EXAMINED WHICH APPEAR TO BLEND CHARACTERS OF *L. macrantha* AND *L. stenoglossa*.—GUATEMALA: Chimaltenango (6 miles west of Tecpán, road to Quezaltenango, White 5226, F, MICH); Huehuetenango (road to San Pedro Soloma, 3 miles southwest of San Mateo Ixtatán, Breedlove 11556, DS, F, MICH; Sierra de los Cuchumatanes, Skutch 1252, F, GH, PH, US; between San Mateo Ixtatán and Cruz de Limón, Sierra de los Cuchumatanes, Steyermark 48500, F; Cruz de Limón between San Mateo Ixtatán and Nucá, Steyermark 49813, F; Cerro Chemal, summit of Sierra de los Cuchumatanes, Steyermark 50295, F, PH); Jalapa (Soledad Montaña Miramundo between Jalapa and Mataquescuintla, Steyermark 32646, F); Quezaltenango (Volcán Zunil, Steyermark 34912, F).

This species is distinguished by its rigidly upright, sparingly branched habit often with a single flowering raceme, more or less sturdy, ascending pedicels, usually large, broadly ovate, cordate, subsessile leaves and bracts with peculiar double marginal incisions, relatively large calyx with broad lobes, apiculate corolla, and the absence of mucros on the base of the anthers. The distribution is scattered in Mexico, and

the plants must be conspicuous for their bright red flowers. Specimens from Oaxaca, including the type, have very large corollas, but like the leaves, they are variable with two extremes in size, some with corollas approximately 30 mm long and others exceeding 60 mm long, these presumed to occur in the same vicinity. The larger flowers appear to have exposed stigmas while the smaller seem to have included stigmas; however, the samples are small and inconclusive. Away from Oaxaca the corollas are more or less intermediate in size.

The leaves and to a certain extent the smaller corollas of *L. macrantha* resemble *L. ovata* so that a number of specimens have been incorrectly labeled. Although poorly known and rare, *L. ovata* shows some characteristics such as reclining stems, nearly right angle branching, depressed inflorescences with inverted flowers which clearly distinguish it from *L. macrantha*. The relationship between these two species probably is more remote than the relationship between *L. macrantha* and *L. stenoglossa*, which is much more surprising since these two at first seem to have so much less in common.

Along the southern border of Mexico between Chiapas and Guatemala in the vicinity of Mt. Tacaná two collections—Matuda 2335, Chiapas, and Beaman 3245, San Marcos—are indistinguishable from *L. macrantha* and establish this species as one of the four that crosses the Isthmus of Tehuantepec, and is one of the two of these exhibiting taxonomic problems in Central America.

Elsewhere in Guatemala in the departments of Chimaltenango, Huehuetenango, Jalapa, and Quezaltenango, several collections appear to combine characters of *L. stenoglossa* and *L. macrantha* so that it is perplexing to provide a name for these morphologically intermediate plants. From a taxonomic point of view, these are neither typical *L. macrantha* nor *L. stenoglossa*, and yet they do not seem likely to be a separate taxon. For the time being, these Guatemalan collections are referred to *L. macrantha*, but it is fully realized that they also share characters with *L. stenoglossa*.

7. *L. stenoglossa* F. W. Hunnewell & L. B. Smith
Contr. Gray Herb. 124: 4, pl. 1, fig. 11-12. 193

TYPE LOCALITY.—“Mexico: Chiapas: . . . Cerro de Huitepeque, alt. 2300 m., 1864-70, Ghiesbreght 70 (GH, TYPE) . . .”

HOLOTYPE.—*Ghiesbreght* 706, GH.

ISOTYPES.—BM, F, K, MO, NY.

Stems erect to 1 m long. Leaves glabrate to pubescent, the larger 22(41)57 mm long, 9(11)15 mm broad, narrowly ovate to lanceolate or elliptical, mostly truncate basally, petiole 1–2 mm long, margins serrate or dentate, often doubly so, the teeth 16–38 on a side, midrib standing out below, the 7–9 laterals on a side faint. Inflorescences ascending; pedicels thin and often somewhat contorted, 9(11)15 mm long. Calyx pubescent, 8(10)12 mm long, 4(5)6 mm broad. Corolla red or red-orange, 39(43)46 mm long, 10(11)12 mm broad, mostly ventricose, the upper lip 12(17)20 mm long, apiculate, little or not galeate, the forward margins rounded, reflexed; the lobes of the lower lip 2–3 mm long, 2–3 mm broad. Stamens subequal or the upper pair shorter, anthers equal in size, shaggy, probably exserted and spreading, little or not mucronate. Capsules ovoid, 11 mm long, 9 mm

broad. (Figure 21). Altitude 2287–2866 m. Flowering: July to September and January.

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 22). MEXICO: Chiapas (Chamula, Zontehuitz, 9400 ft, 30 July 1964, *Breedlove* 6706, DS, ENCB, F, MICH; San Cristóbal las Casas, Zontehuitz, 8770 ft, 19 Jan. 1965, *Breedlove & Raven* 8107, DS, ENCB, F, MICH, US; San Cristóbal las Casas, Zontehuitz, 9300 ft, 20 Sept. 1965, *Breedlove* 12349, DS, F, MEXU, MICH; San Cristóbal near Rancho Nuevo, 9000 ft, 20 Aug. 1966, *Breedlove* 15127, DS, MEXU; Tenejapa, Achlum, 9100 ft, 23 Aug. 1966, *Breedlove* 15179, DS; Tenejapa, Matsab, 25 Aug. 1966, *Breedlove* 15282, DS, MEXU; *Ghiesbreght* "74, 173, 176," GH; *Ghiesbreght* 706, see type; near San Cristóbal, 7000–8000 ft, 18–22 Sept. 1895, *Nelson* 3212, GH, US).

The collections most closely resembling the holotype and paratypes of this species are restricted to Chiapas,



FIGURE 22.—Distribution of section Lamourouxia in Mexico and Guatemala. Localities in Guatemala of specimens appearing to blend characters of *L. macrantha* and *L. stenoglossa* shown by open, five-pointed stars, and localities of glabrate *L. dependens* shown by open squares.

where they are distinct and ought not to be confused with any other taxon. The apparently branched habit with more than one raceme, the erect inflorescence, the apiculate, ventricose corollas on long wiry pedicels, and the often double incisions of the narrow and petiolate leaves will help to confirm this opinion.

This species resembles *L. dependens* and *L. xalapensis*, but is separated from them by the erect inflorescence, hence lack of inverted flowers. At first glance, one would not expect a taxonomic problem with *L. macrantha*, of scattered distribution in Mexico, but now believed also to occur in Guatemala. In general, the better known Mexican collections of *L. macrantha* tend to be less branched with mostly a single raceme that is rigidly erect, the pedicels are more rigid and erect, the flowers and calyx usually are larger, and the leaves broader and more nearly sessile or at least their cordate bases concealing the short petiole. Most of the several Guatemalan collections (unlike the Mexican) bear a strong resemblance to *L. stenoglossa* and thereby diminish the discontinuity between these species. See discussion under *L. macrantha*.

8. *L. ovata* Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12 (2): 33. 1845.

TYPE LOCALITY.—"Dans les montagnes calcaires de Zeta, près de Sola (sud d'Oaxaca), à 8,000 pieds . . . Septembre . . . H. Gal. No. 989."

TYPE SPECIMENS.—*Galeotti* 989, BR, G.

Stems reclining. Leaves pubescent, broadly ovate, 33–58 mm long, 22–37 mm broad, cordate at base and sessile, obtuse, doubly serrate to crenate with 25–31 teeth on a side, veining standing out below with 5–8 laterals. Inflorescence arching forward, the tip depressed, pedicels 6–9(13) mm long, reflexed away from the growing tip, the flowers inverted. Calyx sparsely pubescent, 14–18 mm long, 9–10 mm broad, the lobes 8–11 mm long and 8 mm broad, the sinus folds projecting outward. Corolla red or red-orange, 40–42 mm long, 10–11 mm broad, the upper lip 13 mm long, little or not galeate, the forward margins broadly reflexed. Lobes of the lower lip 6 mm long, 4 mm broad, rounded. Stamens subequal, exserted and spreading, the anthers all fertile and pubescent, the lobes little or not mucronate at base. (Figures 21, 23).

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 22).—MEXICO: Oaxaca (Cerro de San Felipe,

2000 m, 10 Oct. 1897, *Conzatti & Gonzales* 508, GH; Cerro San Felipe, 2000 m, 18 Oct. 1908, *Conzatti* 2273, F; Cerro San Felipe, 2000 m, 20 Sept. 1908, *Conzatti* 2294, F; *Galeotti* 989, see type).

Only four collections of this species are known, the type having come from a locality that is presumed to be south of the city of Oaxaca, while the others are from northeast of the city. The leaves are very broad, cordate, and sessile; the very large calyx is sparsely pubescent with most of the hairs along the major veins and the margins of the lobes. The name *L. ovata* frequently has been misapplied to plants of *L. macrantha*, presumably because of the large, ovate, cordate leaves of the latter. The branches and inflorescences of *L. macrantha* are ascending, while *L. ovata* is reclining with nearly right-angle branching, depressed inflorescences, and inverted flowers. The closest affinity probably is with *L. dependens* of Guatemala.

9. *L. dependens* Benth. in DC. Prod. 10: 539. 1846.

TYPE LOCALITY.—"in Guatimala (Skinner! . . . (v. in herb. Hook.)".

TYPE SPECIMENS.—Skinner, K (two specimens).

SYNONYMY.—

L. dependens Benth. var. *apiculata* Hunnewell & L. B. Smith, Contr. Gray Herb. 124: 4, pl. 1, fig. 8. 1939. Type locality: "Guatemala: Chimaltenango: . . . 'Santa Elena,' alt. 2400–2700 m, Jan. 1933, *Skutch* 154 (US, TYPE . . .)." Holotype: *Skutch* 154, US 1494811. Isotypes: A, MICH, PH.

L. montana Hunnewell & L. B. Smith, Contr. Gray Herb. 124: 4. 1939. Type locality: "Guatemala: Chimaltenango: Volcan Acatenango, alt. 2450 m., Feb. 1937, *Hunnewell* 14856 (G, TYPE)." Holotype: *Hunnewell* 14856, GH.

Stems weak or reclining, to 3 m long. Leaves mostly pubescent, sometimes glabrate, ovate or broadly elliptical, 28(37)56 mm long, 10(17)25 mm broad, rounded or acute apically, blade truncated or obtuse basally, margins doubly serrate or dentate with 12–25 mucronulate teeth on a side; veining standing out below with 4 or 5 laterals; petiole distinct, 3–7 mm long. Inflorescence arching downward, the tip depressed; pedicels 6(10)17 mm long, usually reflexed away from growing tip, the flowers inverted. Calyx mostly pubescent, often glandular, 8(12)16 mm long, frequently one-third or one-fourth the length of the corolla, 5(7)10 mm broad, the lobes 5(8)13 mm long,



1058
Leptosiphon ovata Conzatti
 Cen. San Felipe, Are. in
 Costa Rica
 1950-3300

FIGURE 23.—Section Lamourouxia. *L. ovata*, Conzatti 2273, F.

usually broadly acute, frequently terminally dentate, the axil of the sinuses revolute. Corolla red or red-orange, 36(40)44 mm long, 8 (10)11 mm broad, not galeate, the upper lip 11(13)15 mm long, minutely apiculate or emarginate distally, the lobes obtuse and

strongly reflexed; lobes of the lower lip 2-5 mm long, about 3 mm broad, mostly obtuse. Stamens subequally developed, sparsely pubescent, all fertile, the lobes slightly or not acuminate at base, becoming exserted and spreading. (Figure 21). Altitude: 1950-3300

(?or more) m. Flowering: December to April, peak January to February.

DISTRIBUTION AND NUMBER OF TYPICAL COLLECTIONS EXAMINED (Figure 22).—GUATEMALA: Chimaltenango (9); Huehuetenango (2); Quezaltenango (6); Quiché (3); Sacatepéquez (4); San Marcos (between San Sebastian and San Marcos, Steyermark 35662, F); Sololá (2); Totonicapán (between Quezaltenango and Los Encuentros, *Molina, Burger, & Wallenta* 16416, F, W); and three unknown localities. Doubtful: *Warsiwick* 9, "Costa Rica et Veragua," G.

DISTRIBUTION OF SPECIMENS ANNOTATED AS *L. dependens* BUT REQUIRING SPECIAL COMMENT.—GUATEMALA: Huehuetenango (near San Juan Ixcoy, *Breedlove* 8554, DS, F, US; near San Mateo Ixtatán, *Breedlove* 8766, DS, F, US; Chemal, *Molina, Burger, & Wallenta* 16569, F); San Marcos (near Volcán Tacaná, Steyermark 36329, F; near Aldea Fraternidad, *Williams, Molina, & Williams* 25650, F, NY, US and 26090, BM, F NY, US, W).

This species is recognized by its reclining habit, distinctly petiolate and usually pubescent leaves, depressed inflorescences, inverted flowers, relatively large and often glandular pubescent calyx with frequently dentate lobes, and the exserted and spreading anthers which are only slightly mucronate. The calyx and corollas are very similar to those of *L. ovata*, and both species have dependent inflorescences. The leaves of *L. dependens* are petiolate and relatively narrow, while those of *L. ovata* are very broad, sessile, and clasping. Not only are the leaves very different, but these species also are separated geographically by the Isthmus of Tehuantepec.

The several collections listed above as requiring comment are closest to *L. dependens* but differ because they seem to have somewhat narrower leaves and smaller, glabrate or glabrous calyx. This is perplexing, because characters of the calyx distinguish typical *L. dependens* from other species, and characters of the calyx also distinguish these few specimens from *L. dependens*. These specimens may represent an undescribed taxon; however, for the time being their strongest morphological ties appear to be with *L. dependens*, because there appear to be intermediates. They also resemble *L. xalapensis*; however, if this were their closest specific relationship, they would be the only examples of that species south of the Isthmus of Tehuantepec.

The main character distinguishing *L. dependens* var. *apiculata* was the mucronulate rather than obtuse lobes of the lower lip of the corolla. The main character separating *L. montana* was the minutely emarginate, rather than obtusely cuspidate, termination of the upper lip of the corolla. Another difference now apparent in the latter is the tendency for shorter internodes and a more compact habit. Among the specimens definitely closely allied to *L. dependens*, these characters appear to be of low taxonomic magnitude. Both taxa are included in *L. dependens* and neither, I believe, affects the enigmatic relationship of *L. dependens* to the glabrate form in Guatemala.

10. *L. xalapensis* H.B.K., Nov. Gen. 2: ed. folio 272, ed. quarto 338. "1817," 1818.

TYPE LOCALITY.—"Crescit in declivitate orientali montium Mexicanorum prope urbem Xalapa, alt. 680 hex . . . Floret Februario."

TYPE SPECIMENS.—Xalapa, P (in Humboldt & Bonpland Herbarium and possibly two sheets in General Herbarium, e.g., Herb. Al. de. Bunge, Herb. E. Cosson).

SYNONYMY.—

L. spathacea Bentham in DC. Prod. 10: 539. 1846. Type locality: "In monte Orizaba (Linden! n. 226), in queretis prov. Oaxaca (Galeotti! n. 1007 bis ex parte) . . . (v. in herb. Hook.)." Syntype specimens: *Linden* 226, BR, K; *Galeotti* 1007 bis, BR, K.

L. parviflora W. B. Hemsley, Biol. Cent.-Amer. 2: 465. 1882. Type locality: "Mexico, without locality (Tate, 31; Mairet, 56). Hb. Kew." Syntype specimens: *Tate* 31, K; *Mairet* 56, K.

L. exserta Robinson & Greenman, Amer. Jour. Sci. 50: 171. 1895 (Contr. Gray Herb. 9: 171. 1895). Type locality: "Valley of Mexico, Bourgeau, 986, Schaffner, 367; and in rich ravines of Sierra de Clavellina, Oaxaca, altitude 9,000 feet, 18 October, 1894, Pringle, 4995; also on top of Sierra Madre near Chilpancingo, altitude 9,000 to 10,200 feet, 24 December, 1894, Nelson, 2216, and at Tlalixtaquila, Nelson, 2261." Syntype specimens: *Bourgeau* 986, BR, C, G, K, UC, US; *Pringle* 4995, BR, CAS, G, GH, K, MEXU, MO, MSC, NY, PH, RSA, US, W; *Nelson* 2216, US; *Nelson* 2261, not found; *Schaffner* 367, K, NY, P.

Stems 1–4 m long, weak or reclining. Leaves glabrous or glabrate, infrequently pubescent along major veins and along margins, narrowly lanceolate to ovate, mostly attenuate apically, broadly acute or tapered to the base, 27(48)63 mm long, 6(12)20 mm broad, the petiole 1(3)6 mm long, margins mostly finely

serrate with 20–30 often-mucronulate teeth on a side, veining standing out below and sometimes also above, with 8–11 secondary veins. Inflorescences arching downward, the tip depressed; pedicels filiform, 2(6)12 mm long, usually reflexed away from growing tip, the flowers inverted. Calyx mostly glabrous, 8(9)12 mm long, 4–5 mm broad, the lobes 3(5)7 mm long, entire and usually triangular or calyx sometimes appearing spathiform, 8(15)18 mm long, deeply cleft on the lower side with about 4 narrowly elongate lobes on the upper side. Corolla red or red-orange, 28(40)48 mm long, 8(11)12 mm broad, often appearing slightly arched, the upper lip 9(11)16 mm long, not galeate, often emarginate, the forward margins broadly rounded and reflexed, 4 mm broad, the lobes of the lower lip to 4 mm long. Stamens subequally developed, the anthers shaggy, not mucronate, finally exserted and spreading. Capsules spheroidal to ellipsoidal, 9–10 mm long, 7–9 mm broad. (Figure 21). Altitude: 1220–3350 m. Flowering: July to April, peak November to December. Frequently mentioned as occurring in damp thickets or mixed forests.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED; "s" INDICATES SPATHIFORM CALYX (Figure 22).—MEXICO: Distrito Federal (5); Guerrero (11); Hidalgo (2s); Jalisco (5); State of Mexico (11); Michoacán (Coalcomán, 2500 m, 20 Dec. 1938, *Hinton* 12798, BR, DS, G, MICH, RSA, TEX, UC, US); Morelos (1+1s); Oaxaca (8+5s); Puebla (3+4s); Veracruz (1+8s). See also *L. dependens* for unlikely extension of range to Guatemala.

This species is distinguished by its clambering habit, wide- to nearly right-angle branching, depressed inflorescence tips with reflexed and inverted flowers, usually long lanceolate, glabrous leaves, and glabrous calyx. The calyx is notable for exhibiting two distinctive morphological extremes. In the one, the calyx is more or less equally four-lobed and barely bilabiate; in the other, the calyx tube is narrowly elongated, deeply cleft on the lower side, and more or less laciniate on the upper side. The latter situation appears to be the basis for Bentham's *L. spathacea*. There may be a weak correlation between longer leaves and the longer, spathiform calyxes.

The spathiform calyx is distinctive and perhaps should receive infraspecific taxonomic recognition; however, there is intergradation with the more regular form and sometimes variation on a single specimen. The calyxes on the presumed type specimen at Paris

from "Xalapa" are not well preserved, but they appear to be more or less equally lobed. This species is believed to be restricted to Mexico west of the Isthmus of Tehuantepec. See discussion of unusual specimens, cited under *L. dependens*, which resemble *L. xalapensis*.

II. Section Adelphidion W. R. Ernst, sect. nov. Species 11–14.

Corolla tuba plus minusve infundibuliformis, non ventricosa, subrosea vel lavandulacea vel magentea, non rubro-aurantiaca. Stamina dimorphus, omnia fertilis, inferiora longiores et majores.

Stamens strongly unequal, the anthers dimorphic, the lower pair with somewhat thickened filaments and two large, shaggy pubescent anthers near the mouth of the corolla or barely exposed, the upper pair of stamens shorter, always included, with filiform filaments and smaller, but fertile anthers. Corolla lavender, pink, or magenta (not red), the tube more or less funnelform (Figures 8, 10, 24).

TYPE SPECIES.—*L. dasyantha* (Cham. & Schlecht.) W. R. Ernst.

DISTRIBUTION: Two species in Mexico and two species in northwestern South America (Figures 25, 27).

11. *L. brachyantha* Greenman, Proc. Amer. Acad. 41: 248. 1905 (Contr. Gray Herb. 31: 248 1905).

TYPE LOCALITY.—"State of Mexico: Rocky hills, Lecheria, Valley of Mexico, altitude 2285 m. 1 July, 1904, C. G. Pringle, no. 8815 (hb. Gr.)."

HOLOTYPE.—*Pringle* 8815, GH.

ISOTYPES.—BM, C, CAS, F, G, K, MEXU, MO, MSC, NY, PH, UC, US.

Stems to 1 m tall. Leaves and bracts coriaceous, glandular pubescent, 18(25)35 mm long, 8(13)18 mm broad, ovate, truncate to cordate, sessile, clasping; margins coarsely 9–22 dentate on a side; secondary veins 3–5(9), prominent below. Inflorescence ascending; pedicels 2–4 mm long. Calyx glandular pubescent, 5(8)11 mm long, 5(6)7 mm broad, the lobes broadly triangular, 3(4)6 mm long, conspicuously dentate. Corolla pink or violet (?white), conspicuously galeate, 15(18)22 mm long, 8–11 mm broad; upper lip 5(7)9 mm long, the lobes obtuse, reflexed; lobes of lower lip about 3 mm long, 2–3 mm broad, obtuse. Stamens dimorphic, anthers included, upper

pair smaller, all fertile. Style pubescent, the stigma about 1.5 mm broad, rounded, barely exserted. Capsules 10–12 mm long, 8 mm broad. Altitude: 2200–2800 m. Flowering: July to September. Occasionally on calcareous soil. (Figure 24).

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 25).—MEXICO: Distrito Federal (5); Hidalgo (near Tepiji del Rio, *Straw & Gregory 1170*, RSA); State of Mexico (7); Querétaro (2).

This species is distinguished by the conspicuously galeate corollas which are about as long as broad with broad, open mouth. The anthers remain included, and the relatively large stigma is barely exserted. Greenman (1905) placed this species in section *Hemispadon* next to *L. rhinanthifolia*, presumably because of the similarity of the leaves and calyx. This species probably is not very closely related to any other and is placed with section *Adelphidion* because of the development of the stamens and the non-red, short corolla.

12. *L. dasyantha* (Chamisso & Schlechtendal) W. R. Ernest. comb. nov. Basionym: *Gerardia dasyantha* Chamisso & Schlechtendal, Linnaea 5: 104. 1830.

TYPE LOCALITY.—“Tierra fria. Sept.”

PRESUMED HOLOTYPE.—*Schiede* 165, B, destroyed in war. Pre-war photos F, PH, US (Figure 26). Fragment of original type, PHIL (see Pennell, F. W., Proc. Acad. Sci. Philadelphia 80: 345. 1928; ibid., 81: 246. 1929).

SYNONYMY.—

Lamourouxia linearis Benth. in DC., Prod. 10: 540. 1846. Type locality: “In planicie Mexicana (G.J. Graham! Berlandier! Alaman! Mendez! Galeotti! n. 1007 . . . v.s.)”

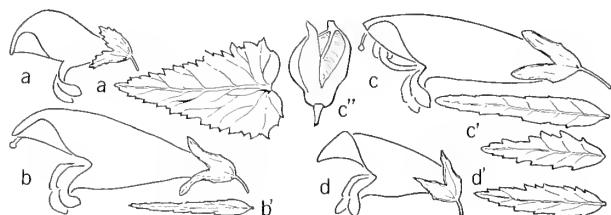


FIGURE 24.—Section *Adelphidion*, diagrams of flowers and leaves. a, *L. brachyantha*, Pringle 13593, US; b, *L. dasyantha*, Pringle 7370, PH; b', Langman 3047, PH; c, *L. virgata*, Haught 3285, US; c', Killip & Smith 17350, US; c'', Dryander 1775, US, capsule; d, *L. sylvatica*, Tovar 164, US; d', Ochoa 348, US.

Syntype specimens: *Graham* 285, plains of Papetonga, BM, K; *Berlandier*, GH, K; *Alaman* (not seen); *Mendez* (not seen); *Galeotti* 1007, BR, G, K, W.

Gerardia punctata Robinson, Proc. Amer. Acad. 26: 172. 1891 (Contr. Gray Herb. 1: 172. 1891). Type locality: “Hills of Zacatecas; October, 1888 (n. 2183).” Type specimen: *Pringle* 2138, GH.

Lamourouxia tenuifolia Martens & Galeotti var. *micrantha* Greenman, Proc. Amer. Acad. 35: 313. 1900 (Contr. Gray Herb. 18: 313. 1900). Type locality: “Collected on the west side of Valley of Cuicatlán, Oaxaca, altitude 2,000 to 2,100 m, by E. W. Nelson, 10 November, 1894, no. 1891. Types in herb. Gray and herb. U.S. Nat. Museum.” Isotypes: *Nelson* 1891, GH, US=L. *dasyantha*, not *L. tenuifolia*.

Stems erect to 1 m tall, frequently branching from below. Leaves glabrous to glabrate, 15(29)32 mm long, 1(3)4 mm broad, subulate to lanceolate, acute to obtuse apically, tapered or rounded to the base, sessile or petiole less than 1 mm long, margins entire to subserrate with 5–9 incisions on a side, sometimes revolute; midrib standing out below. Inflorescences ascending, pedicels 2(3)4 mm long. Calyx glabrous to glabrate, 9(11)13 mm long, 3 (4)5 mm broad, the major veins standing out, the lobes broadly subulate, 5(7)10 mm long; occasionally with a short, fleshy appendage in the axil of the sinus. Corolla pink, lavender, mauve, purplish, 27(32)35 mm long, 8(9)11 mm broad, little or not galeate, the upper lip 8(10)13 mm long, the lobes obtuse, strongly reflexed; the lobes of the lower lip obtuse, 3–5 mm long and broad. Stamens dimorphic, all anthers fertile, the smaller pair always included, the larger pair sometimes barely exposed, loosely connivent or spreading. Capsules 10 mm long, 6 mm broad. Altitude: 1200–3000 m. Occasionally on limestone. Flowering: July to December, peak October to November. Figures 24, 26.)

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 25).—MEXICO: Coahuila (Cárneros Pass, *Pringle* 3682, GH); Distrito Federal (12); Hidalgo (12); State of Mexico (17); Michoacán (3); Nuevo León (14 miles north of Matehuala, *Ripley & Barneby* 13292, CAS, NY); Oaxaca (12); Puebla (10); Querétaro (mountains of Querétaro, *Bruff* 1085, MEXU); San Luis Potosí (10); Tlaxcala (2); Zacatecas (6).

This species is distinguished by the tufted or branching habit, the long, narrow, essentially glabrous and entire, or obscurely serrated leaves, and the large palate which nearly occludes the corolla mouth. One



FIGURE 25.—Distribution of section Adelphidion in Mexico.

of the extremes is the lush biotype that Bentham named *L. linearis* which has larger flowers and broader leaves and recalls *L. virgata* of South America. The plants described by Robinson as *Gerardia punctata* usually have smaller flowers with dark, speckled calyx and almost linear, terete leaves in the dried condition. Approximately intermediate are those plants matching the fragment and the photo of the type of *Gerardia dasyantha*. These variations are conspicuous, but I believe they are best combined until there is biosystematic evidence to the contrary. Specimens have been misidentified frequently in herbaria as *L. tenuifolia*, presumably because the leaves are similar, but this is a valid name for a distinctive species in section Hemispadon. Greenman's trinomial *L. tenuifolia* var. *micrantha* is an example of this confusion and his type specimen for the varietal name is equivalent to *L. dasyantha*.

13. *L. sylvatica* H.B.K., Nov. Gen. 2: ed. folio 272, ed. quarto 337. "1817," 1818.

TYPE LOCALITY.—"Crescit in sylvis prope pagum Ayavaca Peruvianorum alt. 1400 hex . . . Floret Augusto."

TYPE SPECIMEN.—Ayavaca, n. 3465, P (in Humboldt & Bonpland Herbarium, and in General Herbarium).

SYNONYMY.—

L. breviflora Bentham in DC. Prod. 10: 540. 1846. Type locality: "In Peruviae prov. Chachapoyas (Mathews! n. 2119 et 3138 . . . (v.s.))" Syntype specimens: Mathews 2119, K; Mathews 3138, BM, G, GH, K.

L. subincisa Bentham in DC. Prod. 10: 540. 1846. Type locality: "In Andibus Quitensium (Jamison!) . . . (v. in herb. Hook.)." Type specimens: Herb, Hook. "Andes Peru McLean," K; Herb. Benth. "Andes Hooker Jamison 1845," K.

Stems to 70 cm tall, perhaps longer. Leaves pubescent, sometimes scabrous or rugose, to glabrate and smooth, the larger 29(33)44 mm long, 6(9)14 mm broad, often smaller, elliptical, lanceolate or oblanceolate, broadly attenuate basally, the margins shallowly to deeply 3-17 serrate or dentate on a side, the teeth obscure to 2 mm long; midrib and/or 3 veins standing

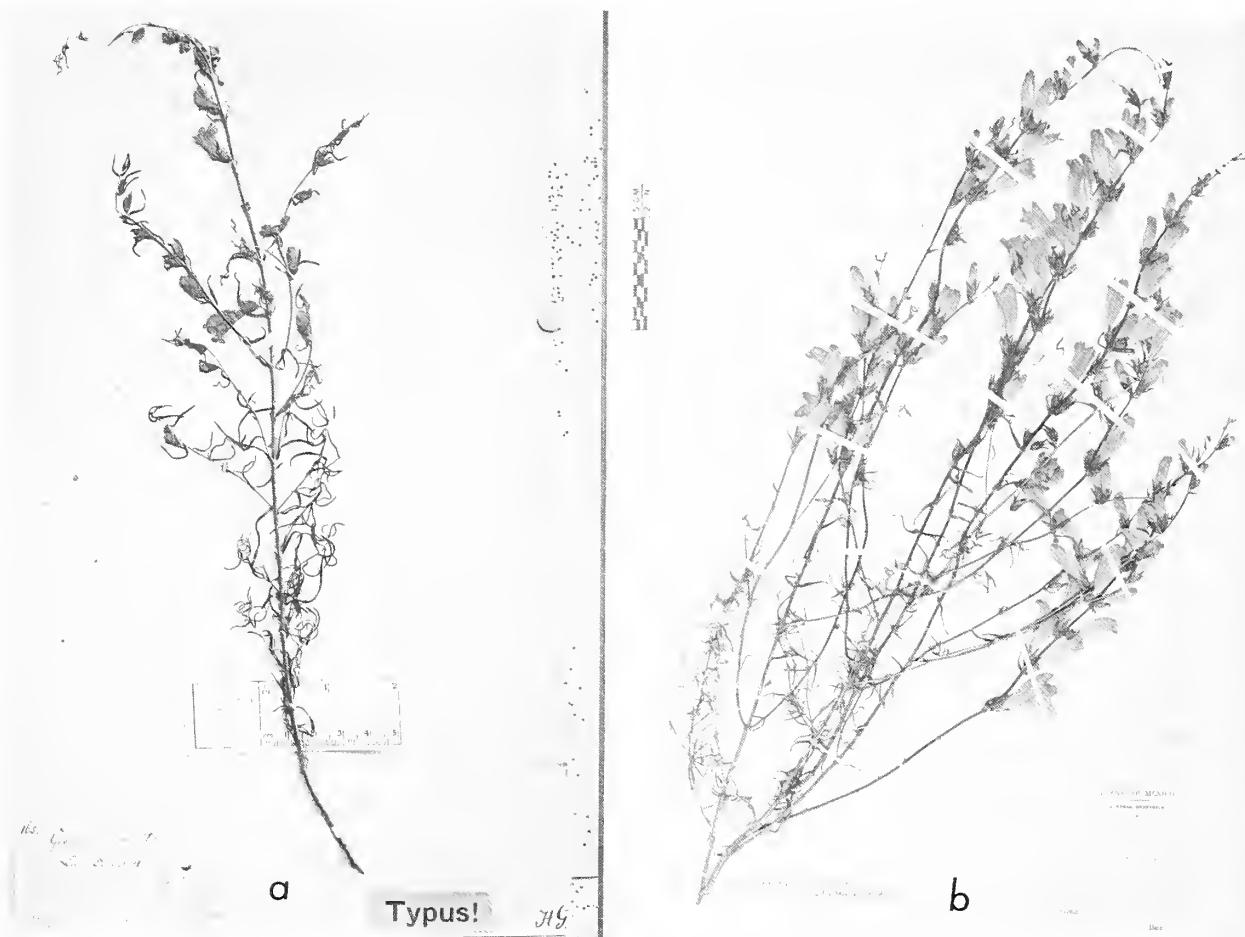


FIGURE 26.—Section Adelphidion. *a*, *L. dasyantha* (presumed holotype of *Gerardia dasyantha*, Schiede s.n., destroyed in Berlin, photo distributed by Field Museum); *b*, similar equivalent, C. L. Lundell 12560, US.

out below, sometimes reticulate. Inflorescences ascending, pedicels 2–3 mm long. Calyx glabrate to scabrous pubescent, 7(9)10 mm long, 4(5)6 mm broad, the lobes triangular, 3(5)7 mm long, sometimes serrate. Corolla rose-pink to purple or white, 13(20)24 mm long, 5(8)9 mm broad, the upper lip 5(7)10 mm long, little or not galeate, the forward margins rounded, reflexed, the lobes of the lower lip 2–4 mm long, 4 mm broad, rounded. Stamens dimorphic, the upper pair shorter, the anthers always included, smaller, usually fertile, the lower pair longer and larger, sometimes exserted. Capsule ovoid, 9–12 mm long, 7–9 mm broad. (Figure 24). Altitude: 2080–3450 m. Flowering: February to July and October, peak April to May.

DISTRIBUTION AND NUMBER OF COLLECTIONS EX-

AMINED (Figure 27).—COLUMBIA: (Lobb, “Columbia,” K, doubtful). ECUADOR: Azuay (3); Cañar (5–8 km NE of Azogues 1 Apr. 1945, Camp 2521, NY). Loja (2). PERU: Amazonas (9); Ancash (9); Cajamarca (11); Huancavelica (Parapuquio below Conaica, 3300–3350 m, 13 Mar. 1951, Tovar 164, US); Junín (4); La Libertad (5 km south of Otuzco, 2600 m, 24 Apr. 1957, Sagastegui 58, US); Pasco (2).

This species probably is closest to *L. virgata* but is distinguished by the corollas which are consistently smaller with proportionately larger palates. The leaves are exceedingly variable and, although mostly smaller, the larger ones exceed those of *L. virgata*. In habit, some specimens resemble the South American species of the genus *Bartsia*; however, this probably is only



FIGURE 27.—Distribution of section Adelphidion in South America, showing range of *L. virgata* in Colombia and Ecuador, and *L. sylvatica* in southern Ecuador and Peru.

coincidental as the latter have very different seed characteristics.

The name *L. sylvatica* has been ignored because the original description did not seem convincing, the species was not illustrated, and the type is incomplete. Both "subvolubilis" and "volubilis" appeared in the description, but I believe this was an exaggeration. The stems of some species of *Lamourouxia* are not strong and longer ones, including those of *L. sylvatica*, probably are supported by surrounding vegetation. The stems of at least three species in North America are so weak as to arch through and over other vegetation, but even these do not twine. The original description concluded with "Specimina supertentia carie valde destructa." The presumed type in Paris has capsules, but there are only a few fragments of bracts or leaves and no flowers. The geographic locality, "Prope pagum Ayavaca" is in Peru, and I believe south of the range of *L. virgata*. The mostly pubescent calyx suggests the identity of this

taxon as equivalent to Bentham's *L. breviflora* and *L. subincisa*.

Although Bentham placed his *L. breviflora* and *L. subincisa* in two different sections, I find the type specimens sufficiently similar to be conspecific with *L. sylvatica*, hence, originating from Peru or extreme southern Ecuador. Whether this version of *L. sylvatica* includes more than one taxon cannot be answered from herbarium studies at this time, as any noteworthy characters appear to be recombined in other specimens. Pennell had the advantage of collecting *Lamourouxia* in Peru and used at least three additional manuscript names besides Bentham's *L. subincisa* for plants that I refer to *L. sylvatica*. The important point is that *Lamourouxia* exhibits two classes of flowers in South America: the larger are *L. virgata* in Colombia and Ecuador, and the smaller are *L. sylvatica*, in southern Ecuador and Peru. Further subdivision of either species will not change this relationship.

14. *L. virgata* H.B.K., Nov. Gen. 2: ed. folio 270, ed quarto 335, pl. 167. "1817," 1818.

TYPE LOCALITY.—"Crescit prope urbem Quito, alt. 1500 hex . . . Floret Majo."

TYPE SPECIMEN.—Quito, n. 3009, P. (in Humboldt & Bonpland Herbarium and in General Herbarium).

SYNONYMY.—

L. serratifolia H.B.K., Nov. Gen. 2: ed. folio 271, ed. quarto 336, pl. 168. "1817," 1818. Type locality: "Crescit juxta Santa Fe de Bogota et catarractam Tequendamae in Regno Novo-Granatensi, alt. 1360 hex . . . Floret Junio." Type specimens: Santa Fe de Bogota, Bonpland, P (in General Herbarium, three specimens, not in Humboldt & Bonpland Herbarium), F, US.

L. loxensis Benthams, Plantae Hartwegiana, p. 147. 1844. Type locality: "In montibus Loxa." Type specimens: Hartweg 824, K (two specimens).

Stems to 2.5 m tall. Leaves glabrous to pubescent, 19(26)31 mm long, 2(5)8 mm broad, lanceolate to elliptical, mostly acute, broadly attenuate basally, mostly without distinct petiole; finely to coarsely 2-9 serrate on a side, the teeth to 2 mm long; midrib standing out below, the laterals inconspicuous. Inflorescence ascending, the pedicels 3(4)6 mm long, sometimes secund. Calyx glabrous to finely pubescent, 9(11)14 mm long, 4(6)8 mm broad, major veins often standing out, the lobes triangular, 5(7)10 mm long, occasionally serrate. Corolla pink or violet to magenta, sometimes "red" or purple, 29(38)45 mm long, 8(11)13 mm broad, the upper lip 8(12)17 mm long, little or not galeate, the forward margins rounded and reflexed, the lobes of the lower lip to 5 mm long, 4-5 mm broad. Stamens dimorphic, the upper pair shorter, always included, the anthers small but mostly fertile, the lower pair usually partly exposed, shaggy, the lobes short mucronate below, the filaments thickened. Capsules ovoid, to 15 mm long, about 8-9 mm broad. (Figure 24). Altitude: 1800-3821 m. Flowering: throughout the year, peak April to October.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 27).—COLOMBIA: Boyacá (2); Cauca (18); Cundinamarca (18); Nariño (17); Norte de Santander (2); Santander (3). ECUADOR: Azuay (2); Bolívar (2); Cañar (5); Carchi (6); Chimborazo (7); Imbabura (2); Loja (see type for *L. loxensis*); Pichincha (17); Tungurahua (3). PERU: Very doubtful, "Pavon, 1827, Peru," G.

This species is recognized in South America by the

large size of the flowers, and by the usually broad, glabrate leaves and calyx. Plants from the northern part of the distribution, especially in Colombia, often have more conspicuously serrate leaves, and were described in H.B.K. as *L. serratifolia*. There appears to be no consistent difference to mark *L. serratifolia* or *L. loxensis* Benthams as separate species. In a general way, *L. virgata* probably is closely related to *L. sylvatica*, but the flowers of the former are about twice as long, and the leaves seem to have their own patterns of variation. It is doubtful that a taxonomic problem will arise with these two species, since their ranges of distribution probably do not, or only barely, overlap.

The similarity between *L. virgata* and *L. dasyantha* is difficult to evaluate. Were the labels removed from some specimens, it would at first be difficult to decide whether their origins were Mexico or South America. The similarities are manifest in the appearance of the flowers and the leaves. The plants of the Mexican species, however, are shorter, frequently tufted or branched from below; the flowers are shorter, the palate larger, the lower pair of anthers smaller; the leaves mostly are narrower. Whether the similarity is one of close genetic similarity or morphological convergence is not clear.

III. Section Hemispadon Benthams in DC. Prod. 10
540. 1846. Species 15-26.

Stamens strongly unequal, the anthers dimorphic, the lower pair with thickened filaments, and the 2 large anthers connivent by means of shaggy pubescence barely exposed at mouth of corolla, not spreading short mucronate below; the upper pair of stamens shorter, always included, with filiform filaments and rudimentary, usually glabrate, sterile anthers, or the anthers very small, 1- or 2-celled, rarely producing little pollen. Corolla red or red-orange, rarely pink or white, the tube more or less cylindrical, sometimes slightly doubly ventricose (Figures 8, 11, 28, 34).

LECTOTYPE SPECIES.—*L. viscosa* H.B.K.

DISTRIBUTION.—Twelve species, northern Mexico to central Panama (Figures 29, 30, 33).

15. *L. nelsonii* Robinson & Greenman, Amer. Jour. Sci. 50: 174. 1895 (Contr. Gray Herb. 9: 172. 1895).

TYPE LOCALITY.—“Six miles above Dominguillo, Oaxaca, altitude 4,500 to 5,000 feet, 30 October, 1894, Nelson, 1833.”

TYPE SPECIMEN.—Nelson 1833, US 566389.

Stems erect, to 1.5 m long, more or less viscid glandular pubescent throughout. Leaves ovate to lanceolate, drying membranous, the larger 26(42)71 mm long, 8(11)15 mm broad, mostly sessile and truncate or cordate at base, sometimes appearing as though narrowed to the base, margins variously serrate to dentate or almost crenate with 8–14 teeth on a side, midrib prominent below, sometimes with 2 to several more or less obscure lateral veins. Inflorescences ascending, the pedicels 2(4)8 mm long. Calyx glandular pubescent, 8(13)18 mm long, 4(5)7 mm broad, the lobes mostly narrowly triangular to oblanceolate, extremely variable, 4–24 mm long, sometimes with irregular margins. Corolla red (to pinkish vermillion with lower lip pinkish purple), 6(52)63 mm long, 5(7)9 mm broad, the upper lip 2(19)23 mm long, little or not galeate, the lobes lightly cuspidate, reflexed, the lobes of the lower lip 2–3 mm long. Stamens dimorphic, the upper pair rudimentary, the lower with expanded filaments and baggy, mucronate anthers. Capsules ovoid, to 17 mm long, 8 mm broad. (Figure 28). Altitude: 900–2205 m. Flowering: May to December, peak July to August.

6. *L. viscosa* H.B.K., Nov. Gen. 2: ed. folio 272, ed. quarto 338. “1817,” 1818.

TYPE LOCALITY.—“Crescit in litore Mexicano Oceani Pacifici prope Acapulco . . . Floret Martio.”

TYPE SPECIMEN.—Acapulco, P (in Humboldt & onpland Herbarium and in General Herbarium).

SYNONYMY.—

cordata Schlechtendal & Chamisso, Linnaea 5: 103. 1830. Type locality: “Inter Tenestepeque et Quantotalapa. Sept.” Type specimen: Schiede & Deppe 161, W.

viejensis Oersted in Bentham & Oersted, Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjöbenhavn 1853: 28. “1854,” probably 1853. Type locality: “November paa Vulkanen Viejo i Nicaragua (3000’).” Type specimen: Oersted 9401, C.

coccinea A. Gray, Proc. Amer. Acad. 21: 404. 1886. Type locality: “Rocky hills near the city of Chihuahua, Pringle, 656.” Type specimens: Pringle 656, BR, F, G, GH, K, PH, RSA, US.

ilvesia sessilis M. E. Jones, “Extracts” Contr. Western Bot. 18: 51. 1933. Type locality: “No. 27410 La Bar-

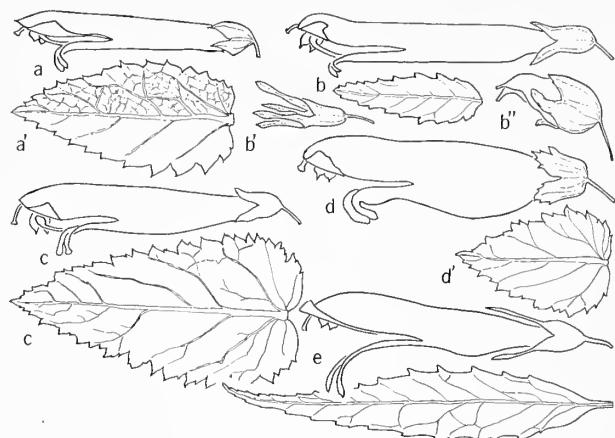


FIGURE 28.—Section Hemispadon, diagrams of flowers and leaves. *a*, *L. viscosa*, Ernst 2442, US; *a'*, Pringle 11654, US; *b*, *L. nelsonii*, Pringle 9334; *b'*, Pringle 6331, US, elongated calyx; *b''*, Pringle 6773, US, capsule with calyx; *c*, *L. smithii*, Pringle 6705, US; *d*, *L. rhinanthalifolia*, Pringle 11064, MICH; *d'*, Stanford, Lauber, & Taylor 2392, MO; *e*, *L. jaliscana*, McVaugh 14250, MICH.

anca, Guadalajara, No. 21. 1920.” Type specimens: Jones 27410, 21 Nov. 1930, GH, NY, date mixed. See Pennell in Morton, Contr. U.S. National Herb. 29: 91. 1945.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 29).—MEXICO: State of Mexico (Coatepec near Villa Guerrero, Gilly, Alexander, & Hernandez 59, MO, MSC); Morelos (2); Oaxaca (5); Puebla (15).

This species is very distinctive but variable and difficult to characterize. The apparently membranous, narrow, and abundantly glandular leaves frequently with widely spaced teeth, the short lobes of the lower lip of the corolla, the highly variable calyx lobes, and the long attenuated capsules help to identify this species. It probably is closest to *L. viscosa*.

Plants to 3 m tall. Leaves mostly glandular pubescent, coriaceous, sessile, the larger 27(66)112 mm long, 10(26)53 mm broad, broadly or narrowly ovate to elliptical or lanceolate, acute or rounded apically, truncate or cordate basally; serrate to doubly serrate to nearly dentate, the teeth often mucronulate, 14–27 on a side, tertiary veining conspicuously reticulate and usually standing out below. Inflorescences ascending; pedicels 2(3)6 mm long. Calyx mostly glandular pubescent, 5(7)8 mm long, 4(5)7 mm broad, the lobes triangular, about as long as the cup, 2(3)4 mm



FIGURE 29.—Distribution of section *Hemispadon* in Mexico and Central America.

long. Corolla red, sometimes tinted orange, salmon, pink, or purple, 30(46)60 mm long, 4(6)12 mm broad, upper lip 12(18)27 mm long, mostly not galeate, the forward margins rounded cuspidate, slightly reflexed, the lobes of the lower lip 1–3 mm long, 1–2 mm broad. Capsules ovoid, 8–12 mm long, 6–7 mm wide. (Figure 28). Altitude: Mexico, 450–2800 m; Guatemala, 600–2400 m. Flowering: Throughout year, more common September to December.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 29).—MEXICO: Aguascalientes (*Hartweg* 189, G, GH, W); Chiapas (24); Chihuahua (9); Durango (5); Guererro (11); Jalisco (24); State of Mexico (11); Michoacán (11); Morelos (4); Nayarit (10); Nuevo León (near Dulces Nombres, 2000 m, 8 Aug. 1948, *Meyer & Rogers* 2879, BR, G, MO, PH); Oaxaca (24); Puebla (Pahuatlán, 15 Sept. 1945, *Miranda* 3692, MEXU); San Luis Potosí (2); Sinaloa (Mesa Malqueson, Cerro Colorado.

2500 ft, 8 Dec. 1939, *Gentry* 5168, DS, GH, MO, PH, UC); Sonora (10); Tamaulipas (4); Veracruz (13). GUATEMALA: Chimaltenango (Alameda, *Johnsto* 315, F); Chiquimula (Volcán Ipala near Amatill 900–1510 m, 25 Oct. 1939, *Steyermark* 30571, F); Escuintla (2); Guatemala (5); Huehuetenango (5); Jalapa (3); Jutiapa (3); Quiché (2); Sacatepéque (3); San Marcos (between San Marcos and Castali 1600–2200 m, 16 Dec. 1963, *Williams*, *Molina* *Williams* 26143, F); Santa Rosa (near Cuilapa, 900–950 m, 24 Nov. 1940, *Standley* 78131, F); Sololá (3); Zacapa (2). BELICE: El Cayo (3). EL SALVADOR: Chalatenango (Cerro Roblar, Nov. 1928, *Cederon* 2475, F); Chalchuapa (2); Santa Ana (near Santa Ana, 655–900 m, Jan. 1922, *Standley* 2039, GH, US). HONDURAS: Choluteca (near San Marcos, 1000 m, 16 Nov. 1946, *Williams* & *Molina* 10886, F, GH); Copán (between Llave de la Puer and El Salto, 900 m, 10 Jan. 1907, *Pittier* 1852, US); El Paraíso (2); Morazán (9); Santa Bárbara (Sa-

Pedro Sula, 600 m, *?Thieme*, US). NICARAGUA: Chinandega (3); Jinotega (near Jinotega, 1030–1300 m, June–July 1947, *Standley* 9873, F); plus 4 uncertain. COSTA RICA: Alajuela (near San Ramón, 1025 m, 8 Nov. 1926, *Brenes* 2134, F); Cartago (3); Heredia (Alto de Santa Bárbara, 1400 m, 21 Dec. 1889, *Pittier* 1666, BR); Puntarenas (2); San José (Cerro de Pralti Escasú, 1300 m, Aug., 1935, *Solis* 318, F, MO). PANAMA: Chiriquí (between Cerro Vaca and Hato del Loro, 850–1100 m, 27 Dec. 1911, *Pittier* 5398, US; Valle de Antón, 800 m, 8 Sept. 1941, *Allen* 2235, MO, US).

CHROMOSOMES.— $n=14$, counted by Ernst from *D. E. Breedlove* 18676, Jalisco, 16 miles northwest of Ameca along the road to Mascota, 4300 ft, 1 Nov. 1970, CAS, US.

With more than 250 separate collections, this is the most frequently collected and the most variable species, as would be expected for a taxon distributed from northern Mexico to central Panama. The broad, coarse, mostly conspicuously reticulately veined leaves with cordate base usually separate this from all other species. Sometimes the leaves are narrow and appear tapered to the base. This species probably is closely related to the uncommon *L. nelsonii* and to *L. rhinanthifolia*, which is very common in Mexico and at times appears to have overlapping characters suggesting the possibility of hybridization. The thick leaves, glandular calyx, and narrow, more pointed corollas usually distinguish *L. viscosa* from *L. rhinanthifolia* which generally has thinner leaves, mostly nonglandular calyx with incised lobes, and broader, often more blunt corollas; both species sometimes have scabrous leaves. The corollas of *L. viscosa* in Chiapas are unusually broad; however, *L. rhinanthifolia*, with which these plants might be confused, does not cross the Isthmus of Tehuantepec. The habitats most frequently mentioned are grassland openings in arid oak and/or pine forest, sometimes on limestone, near cultivation, or in *Acacia*-*Yucca*-cactus woodland.

17. *L. rhinanthifolia* H.B.K., Nov. Gen. 2: ed folio 271, ed. quattro 337. pl. 169. "1817," 1818.

TYPE LOCALITY.—"Crescit locis temperatis Novae Hispaniae prope pagos Magdalena, Actopan et Sancta Rosa de la Sierra, alt. 1040–1300 hex . . . Floret Julio–Septembri . . . Descriptio speciminis propter agum Magdalena lecta . . ."

TYPE SPECIMEN.—S. Rosa, n. 4274, P (in Humboldt & Bonpland Herbarium).

Stems erect to 1 (3) m tall. Leaves membranous and pubescent to coriaceous and scabrous, the larger 16(34)52 mm long, 11 (17)28 mm broad, sessile, mostly ovate or elliptical, rounded or obtuse apically, truncated to cordate basally, serrate to doubly serrate or nearly dentate, the teeth 8–21 on a side, sometimes mucronulate; midrib standing out below with a few laterals. Inflorescence ascending; pedicels 1(3)5 mm long. Calyx pubescent, 7(9)12 mm long, 5(8)11 mm broad, the lobes 3(4)5 mm long, broadly triangular and usually deeply serrate, sometimes entire. Corolla variable red (tinted pink, orange, yellow, purple), 47(57)68 mm long, 8(10)13 mm broad, often subventricose toward calyx, upper lip 15(22)26 mm long, little or not galeate, forward margins mostly rounded, reflexed; the lobes of lower lip to 4 mm long. Stamens dimorphic, the upper pair of anthers vestigial, lower pair shaggy, the filaments expanded, and the lobes of the anthers short mucronate. Capsules ovoid, to 13 mm long, 8 mm broad. (Figure 28). Altitude: 793–3110 m. Flowering: May to October, peak June to August.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 30).—MEXICO: Aguascalientes (*Hartweg*, BR); Coahuila (La Casita, *Kenoyer & Crum* 3118, A, MICH); Distrito Federal (13); Durango (13); Guanajuato (3); Hidalgo (5); Jalisco (near Hacienda Chinampas, *McVaugh* 17027, MICH); State of Mexico (27); Michoacán (near Coalcomán, *Hinton* 12356, DS, GH, MEXU, MICH, US); Nuevo León (10); Oaxaca (19); Puebla (8); San Luis Potosí (8); Sinaloa (2); Tamaulipas (4); Veracruz (2); Zacatecas (2).

After *L. viscosa* and *L. multifida*, the third most common species is *L. rhinanthifolia*. The broad, ovate, usually membranous leaves with relatively close, deep, and plentiful teeth, with conspicuous venation below; the broad, serrate sepals; and the relatively broad corollas identify this species. The thick flower tubes recall those of *L. tenuifolia* but these species otherwise are only remotely similar. This species probably is closest to *L. viscosa* but is distinguished by its usually smaller and more membranous leaves, serrate calyx lobes, and broader corollas; however, the two sometimes are confusingly similar. The relationship to *L. smithii* probably also is very close. Limestone substrate is mentioned for Nuevo León, San Luis Potosí, and Tamaulipas.

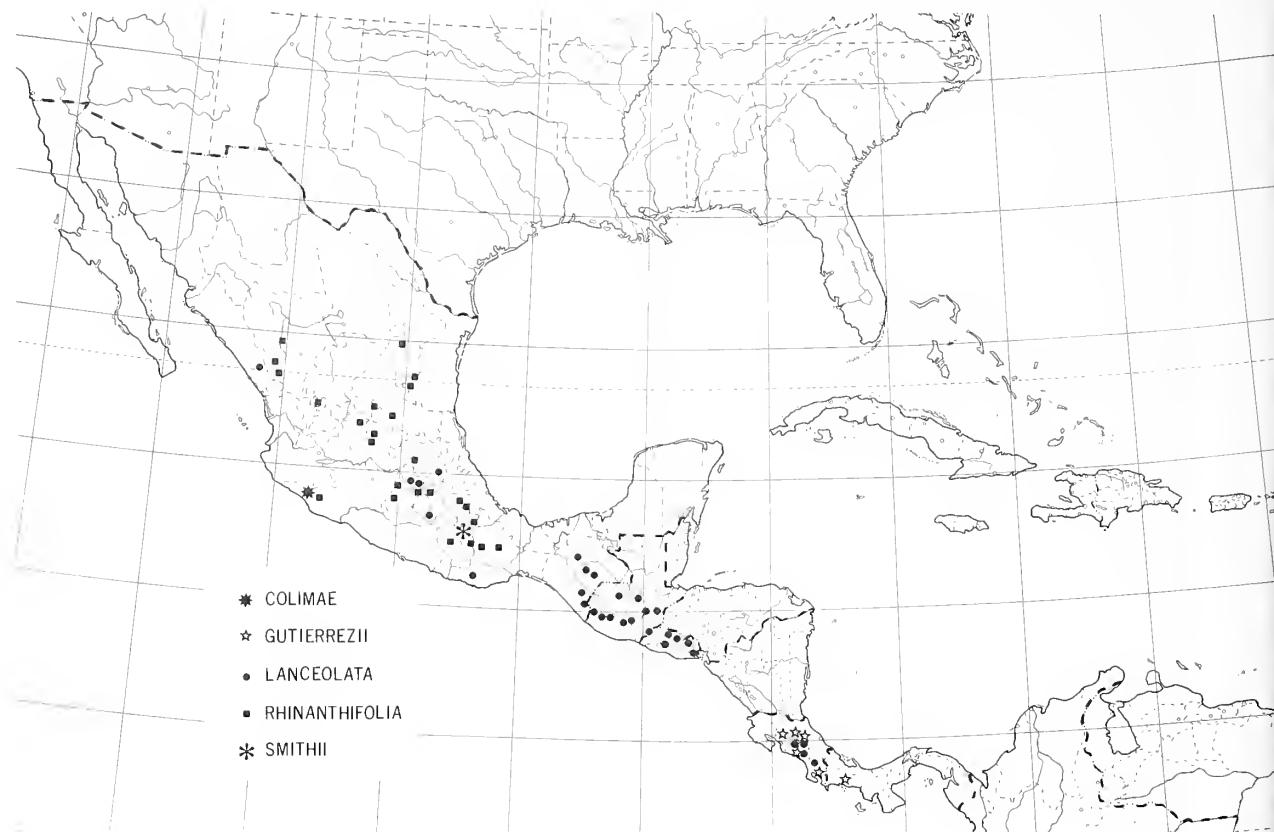


FIGURE 30.—Distribution of section Hemispadon in Mexico and Central America.

18. *L. smithii* Robinson & Greenman, Amer. Jour. Sci. 50: 172. 1895 (Contr. Gray Herb. 9: 172. 1895).

TYPE LOCALITY.—“Mountains of Jayacatlan, Oaxaca, altitude 5,000 feet, 13 August, 1894, L. C. Smith, 155.”

TYPE SPECIMEN.—*Smith 155, GH.*

Stems erect, probably 1 m tall. Leaves pubescent, membranous, ovate, 50(65)72 mm long, 29(35)38 mm broad, sessile and conspicuously cordate basally; margins dentate to serrate, sometimes doubly so, the projections 12–27 on a side, 2–4(6) mm long, often mucronulate; midrib conspicuous above and standing out below with 4–6 laterals. Inflorescences ascending; pedicels 3–5 mm long. Calyx pubescent, 8(10)11 mm long, 5–6 mm broad, the lobes 4–6 mm long, narrowly triangular. Corolla presumed red (or orange), 44(49)54 mm long, 8(9)10 mm broad, the upper lip 17(19)22 mm long, little or not galeate, the forward margins rounded or slightly cuspidate, slightly reflexed; the lobes of the lower lip about

2 mm long. Stamens dimorphic, the upper pair of anthers vestigial, the lower pair shaggy, the lobes mucronate at base, the filaments expanded (Figure 28).

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 30).—MEXICO: Oaxaca (*Smith 155*, see type; Tomellín Canyon, 5000 ft, 17 July 1897, *Pringle 6705*, BR, F, G, GH, IPN, MBG, MEXU, MSC, PH, UC, US, W; Cuicotlan, 580 m, 3 Aug. 1872, *Urbina sn*, MEXU).

This species is distinguished by its membranous, large, cordate, sessile, ovate leaves with their conspicuous, widely spaced venation, and the restricted distribution in Oaxaca. This species seems related to *L. viscosa*, but is especially close to *L. rhinanthifolia*. The leaf size and shape resemble the former; the texture and venation of the leaves and the broadness of the flowers resembles the latter. Little variation is shown by the few collections available; however, it would seem likely that if this species were variable it would blend into *L. rhinanthifolia*.

19. *L. jaliscana* W. R. Ernst & M. F. Baad, Madero 20: 344. "1970," 17 March 1971.

TYPE LOCALITY.—Jalisco: Sierra de Caule, southwest of Talpa de Allende; southwest of Piedra Ra-

jada; elevation 1800–2250 m, 19–21 November 1952.

HOLOTYPE.—Rogers McVaugh 14250 (& J. Sooby, Jr.), MICH (Figure 31) and Isotype.

Stems erect to 1.5 m tall. Leaves possibly scabrous above, soft pubescent below, narrowly lanceolate, 50–



FIGURES 31.—Section Hemispadon. *L. jaliscana*, holotype, McVaugh 14250, MICH.

80 mm long, 6–10 mm broad, attenuate apically and basally, revolute, serrate with 12–22 coarse teeth on a side. Inflorescences ascending; the pedicels 5–8 mm long. Calyx glandular pubescent, 14–16 mm long, 5 mm broad, the lobes narrowly subulate, 10–12 mm long. Corolla red, cylindrical, 56–63 mm long, 9–10 mm broad, the upper lip 16–25 mm long, little or not galeate, the lobes broadly attenuate, 5–7 mm long, reflexed; the lobes of the lower lip narrow, 5–8 mm long. Upper pair of stamens half as long as corolla, the anthers vestigial and glabrous; lower pair of stamens nearly as long as corolla, the filaments dilated distally, the anthers shaggy pubescent, the lobes acuminate at base. Style with spreading hairs. Capsules ovoid, 12–13 mm long, 7–8 mm broad. (Figure 28).

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 33).—**MEXICO:** Jalisco (see type; 11–12 miles south of Talpa de Allende, headwaters of west branch of Río de Talpa, elevation 1200–1700 m, 23–25 November 1960, *McVaugh* 21325 (& C. Feddema, R. Pippen), MICH.).

This species, known from only two collections, is distinguished by its large leaves, subulate glandular calyx lobes, and large corolla. The lower lip of the corolla arches downward with three elongated lobes resembling section Lamourouxia, and the subulate calyx lobes resemble the similar condition in *L. longiflora* and *L. multifida*. The dimorphic stamens with only one pair of fertile anthers, however, establishes this species in section Hemispadon in a more or less central position between extremes. The pubescent leaves and glandular calyx allies *L. jaliscana* to the *L. viscosa* complex; however, the narrowly elongated leaves with their tapered or petiolelike bases resembles the similar condition among the glabrous-glabrate species such as *L. lanceolata* and *L. tenuifolia* (Figure 32).

The position of *L. jaliscana* is enigmatic. The broad corolla, its dangling lower lip with long, spreading lobes and the more or less open mouth clearly suggest an alliance with section Lamourouxia. The heavy, almost scabrous pubescence of the leaves, the glandular condition of the calyx, and the strongly dimorphic stamens with only two fertile anthers, on the other hand, fixes this species in section Hemispadon near the *L. viscosa*–*L. rhinanthifolia* complex. Although the leaves are pubescent and the calyx glandular, the lanceolate, petiolate condition of the leaves recalls the similar characters among the glabrous-glabrate species

of Hemispadon. The position of this species in Hemispadon parallels that of *L. dispar* in section Lamourouxia, inasmuch as either the corollas or the stamens in these two species appear to have become associated with the wrong plants.

20. *L. gracilis* Robinson & Greenman, Amer. Jour. Sci. 50: 174. 1895 (Contr. Gray Herb. 9: 174. 1895).

TYPE LOCALITY.—“Summit of Sierra Madre near Chilpancingo, Guerrero, altitude 9,000 to 12,000 feet, 24 December, 1894, Nelson, 2234.”

TYPE SPECIMENS.—*Nelson* 2234, GH, US.

Stems erect 25–60 cm tall. Leaves membranous, elliptical to obovate, 21(24)28 mm long, 5(7)10 mm broad, basally attenuate, glabrous or with a few appressed hairs; margins sometimes revolute, serrate or almost crenate, with 5–9 teeth on a side, the projections to 1 mm long; midrib standing out below, usually with 3–4 laterals. Inflorescences ascending with few flowers; pedicels 6–10 mm long. Calyx 5(7)9 mm long, 3(4)5 mm broad, glabrate, the lobes broad, oblanceolate, spreading, about 4 mm long, 2 mm broad, sometimes with 2–3 shallow indentations. Corolla “red with yellowish throat,” 45(46)49 mm long, 8(9)10 mm broad, upper lip 14(15)17 mm long, rounded, slightly galeate, the short lobes reflexed; lobes of the lower lip 2–3 mm long. Stamens dimorphic, the upper pair rudimentary, the lower pair with thickened filaments and shaggy anthers, their lobes mucronulate below. Capsule ovoid, 10 mm long, 6 mm broad. (Figure 34.) Flowering: September to December.

COLLECTIONS EXAMINED (Figure 33).—**MEXICO:** Guerrero (see type); Morelos (near Cuernavaca, *Pringle* 6510, BR, CAS, ENCB, F, G, GH, K, MEXU, MO, MSC, PH, UC, US, W; near Cuernavaca, *Pringle* sn, 19 Oct. 1900, C).

This species is distinguished by its small, but elongated, petiolate, glabrate, membranous leaves, broad, reflexed, calyx lobes, and broad corolla. It appears to be closest to *L. microphylla*.

21. *L. microphylla* Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12(2):31. 1845.

TYPE LOCALITY.—“Dans les bois humides de Yolo tepeque et Sola (cordillère au sud d’Oaxaca), de



FIGURE 32.—Section Hemispadon. *L. tenuifolia* (a syntype specimen of *L. conzatti*, Gonzales & Conzatti 760, GH).

6,500 à 7,500 pieds . . . Septembre . . . H. Gal. No 1005."

TYPE SPECIMENS.—*Galeotti 1005*, mixed data representing two or three collections, BR (two specimens), G, K (two specimens), W.

SYNONYMY.—

L. parvifolia Bentham in DC. Prod. 10: 542. 1846. Type locality: "In sylvis prov. Oaxaca (Galeotti. n. 1005) . . .

(v. in herb. Hook.)". Type specimens: *Galeotti 1005*, BR (two specimens), G, K (two specimens), W.

Stems erect to 1 m tall. Leaves glabrous, probably coriaceous, 6–10 mm long, 2–3 mm broad, elliptical to narrowly obovate, attenuate basally and appearing to have a petiole to 1 mm long; margins revolute, serrate or sinuate, with 3–4 lobes on a side, midrib standing out below, sometimes with 2–3 faint laterals.



FIGURE 33.—Distribution of section Hemispadon in Mexico and Guatemala. Localities in Guatemala of specimens appearing to blend characters of *L. integerrima* and *L. lanceolata* shown by open triangles.

Inflorescences ascending, frequently branched, pedicels about 4 mm long. Calyx glabrous, 5–6 mm long, 3–4 mm broad, the lobes triangular, to 1 mm long. Corolla red, 37–41 mm long, 6 mm broad, the upper lip 16–18 mm long, little or not galeate, the forward margins reflexed, the lobes of the lower lip 2–3 mm long. Stamens dimorphic, the upper pair of anthers rudimentary, the lower pair shaggy, the lobes acuminate below, the filaments expanded. Capsules subspherical, 6 mm long, 5 mm broad. (Figure 34).

DISTRIBUTION AND COLLECTIONS EXAMINED (Figure 33).—**MEXICO:** Oaxaca (*Galeotti* 1005, see type; *Cuesta de S. Pedro el Alto*, 10/42, *Liebmann* 9394, A, C(3), F, NY, US; granitic hills, *Sierra de Clavelinas*, 6000 ft, 19 October 1894, *Pringle* 6000, BR, BM, ENCB, G, GH, K, MEXU, MO, MSC, NY, P, PH, RSA, UC, US, W, WIS. Oak-pine woods, 6900 ft, *Sierra Madre del Sur* south of *Miahuatlán*, 14 Nov. 1966, *Ripley & Barneby* 14640, CAS).

This species is distinguished by its very small, glabrous leaves, glabrous calyx with very short lobes,

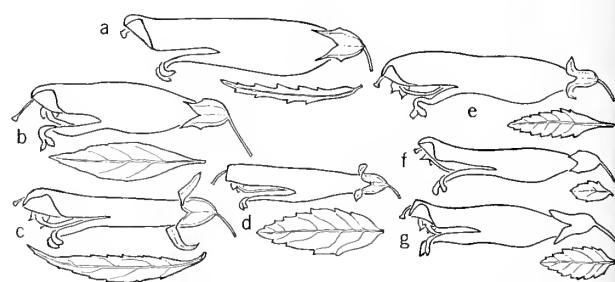


FIGURE 34.—Section Hemispadon, diagrams of flowers and leaves. *a*, *L. tenuifolia*, *Halberg* 939, MICH; *b*, *L. integerrima*, *Steyermark* 43293, F; *c*, *L. lanceolata*, *Tucker* 658, US; *d*, *L. colimae*, *McVaugh* 18077, MICH; *e*, *L. gracilis*, *Pringle* 6510, US; *f*, *L. microphylla*, *Pringle* 6000, US & MEXU; *g*, *L. gutierrezii*, *Allen* 1496, US.

and narrow corollas. There are too few collections for a sense of variation. This species seems most closely allied to *L. gracilis*.

22. *L. tenuifolia* Martens & Galeotti, Bull. Acad. Sci. Bruxelles 12 (2) : 32. 1845.

TYPE LOCALITY.—“Dans les bois de régions tempérées froides de la cordillère orientale d’Oaxaca (San Andreas, Roayaga, etc.), à 6,000 pieds . . . Juin . . . H. Gal. No 922.”

TYPE SPECIMENS.—*Galeotti* 992, BR, G, W.

SYNONYMY.—

L. conzattii Greenman, Proc. Amer. Acad. 35: 312. 1900 (Contr. Gray Herb. 18: 312. 1900). Type locality: “Collected by V. Gonzales and C. Conzatti on the Cerro de Pápaló, camino de Cheve, Cuicatlán, Oaxaca, alt. 2,500 m., 16–22 June 1898, no. 760, and C. Conzatti on the Cerro de Yalina, District of Villa Alta, Oaxaca, altitude 1,500 m., June 1899, no. 965.” Syntype specimens: *Gonzales & Conzatti* 760, GH, US; *Conzatti* 965, GH.

Stems erect, probably 1 m or more tall. Leaves glabrous or glabrate, very narrowly lanceolate or subulate, attenuate at either end, the larger 21(28)32 mm long, 3 mm broad, margins revolute, sinuate to serrate, the teeth 6–10 on a side, usually less than 1 mm long, midrib standing out below or with 3–4 faint laterals. Inflorescences ascending; pedicels 4(5)7 mm long. Calyx glabrous or minutely papillate, 7(9)10 mm long, 3(4)6 mm broad, the major veins usually standing out, the lobes triangular, 4–5 mm long. Corolla red, 45(51)55 mm long, 9(10)13 mm broad, the upper lip 11(16)19 mm long, little or not galeate, margins reflexed, the lobes of the lower lip 2–3 mm long. Stamens dimorphic, the upper pair rudimentary, the lower pair with thickened filaments and shaggy anthers, mucronate below. Capsules 10–12 mm long, 6–8 mm broad. (Figure 34). Altitude: 1372–2500 m. Flowering: April and June to August.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 33).—MEXICO: Oaxaca (near Ixtlán, July 1906, *Conzatti* sn, A, ENCB, G, UC, US, W; *Gonzales & Conzatti* 760, *Conzatti* 965, see syntypes for *L. conzattii*; Sierra de Ixtlán, 2200 m, July 1906, *Conzatti* 1379, ENCB, GH, MEXU; Ixtlán, July 1906, *Conzatti* (or ?Pringle) 10371, F, G, K, MO, MSC, PH; *Galeotti* 992, see type; vicinity of Cerro Zempoaltepec, 2400 m, 13 Aug. 1950, *Hallberg* 939, MICH; Lachopa, 7500–8000 ft, 6/1842, *Lieb-*

mann 9393, C, US, W; Villa Alta, April 1949, *Paray* 122, MEXU).

The very narrow, glabrous leaves, glabrous sepals, and relatively broad corollas distinguish this species, which does not seem to be very closely allied to any of the others. The name *L. tenuifolia* has been misapplied to many collections of *L. dasyantha*, a very different species in section Adelphidion, which, coincidentally, usually has narrow leaves. The type collection for *L. tenuifolia* var. *micrantha* Greenman is *L. dasyantha*.

23. *L. integerrima* J. D. Smith, Bot. Gaz. 13: 189. 1888.

TYPE LOCALITY.—Guatemala, “Pansamala, Alt. 4,000 feet, January, 1887. (Ex Pl. cit. 1112.)”

TYPE SPECIMENS.—*Von Tuerckheim* 1112, G, GH, PH, US (3 sheets) (Figure 35).

Stems to 2.5 m long. Leaves membranous, glabrous or glabrate, lanceolate to narrowly elliptical, attenuate to base, 20(30)42 mm long, 3(5)7 mm broad, margins entire or sinuate or slightly serrate, midrib and a few lateral veins standing out below. Inflorescences ascending; pedicels 4(6)8 mm long. Calyx glabrous or glabrate 7(8)10 mm long, 3(4)5 mm broad, the lobes 2(4)6 mm long. Corolla red, 43(47)51 mm long, 8(9)11 mm broad, the upper lip 14(17)19 mm long, slightly or not galeate, the lobes reflexed; the lobes of the lower lip to 4 mm long. Stamens dimorphic, the upper pair rudimentary, the lower pair with expanded filaments and shaggy anthers, the lobes acuminate basally. Capsules ovoid, 10–14 mm long, 7–8 mm wide. (Figure 34). Altitude: 1220–2865 m. Flowering: December to February and June to October.

DISTRIBUTION AND MORE OR LESS TYPICAL COLLECTIONS EXAMINED (Figure 33).—GUATEMALA: Alta Verapaz (see type); El Progreso (between Finca Piamonte and summit of Volcán Santa Luisa, 2400–3333 m, *Steyermark* 435557, F); Huehuetenango (4 mi E of San Mateo Ixtatán, 8500 ft, *Breedlove* 8768, DS, F, MICH, US; Cerro Cananá near Nucapoxlac, 2500–2800 m, *Steyermark* 49083, F); Quiché (Nebaj, 7600 ft, *Skutch* 1897, A, GH, F, PH, US); Zacapa (between Lomas El Picacho and Cerro de Monos, 2000–2600 m, *Steyermark* 42835; Volcán Gemelos, 2100–3200 m, *Steyermark* 43923, F, PH).

COLLECTIONS PRESUMED CLOSE TO *L. integerrima*, BUT INCOMPLETE OR WITH VERY NARROW AND/OR



FIGURES 35.—Section Hemispadon. *L. integriflora*, presumed holotype, *Von Tuerckheim* 1112, US.

SERRATE LEAVES, AND OFTEN WITH LONGER SEPALS.—GUATEMALA: Alta Verapaz (trail to Senahú, G. P. Goll 116, US); El Progreso (between Finca Piamonte and summit of Volcán Santa Luisa, 2400–3333 m, Steyermark 43475, F, US); Huehuetenango (Cerro Huitz between Barillas and Mimanhuitz, 1600–2600 m, Steyermark 48534, F); Quezaltenango (Volcán Zunil, 2500–3800 m, Steyermark 34588, F; same lo-

cality, Steyermark 34589, F, PH); Sololá (between San Pedro and Volcán Santa Clara, 1900–2100 m, Steyermark 47111, F); Suchitepequez (Volcán Atitlán, 8000 ft, Skutch 1519, A, F, PH, US).

The broad, entire, lanceolate leaves, the ascending inflorescence tips, the short, broad calyx lobes, and the broad corolla distinguish this species. Collections other than the type, however, tend to have narrower

nd often serrate leaves as well as longer calyx lobes. The habit varies and is sometimes noted as shrubby or "drooping." The type collection with its unusual leaves appears to be an extreme condition. The first collections cited above are more or less similar to the type, but the second group is of uncertain relationship, perhaps representing a new taxon or intermediates with *L. lanceolata*. This taxonomic problem is restricted to Guatemala.

4. *L. lanceolata* Bentham in DC. Prod. 10: 542. 1846.

TYPE LOCALITY.—"In Mexici prov. Chiapas ad Matenango (Linden! n. 198) . . . (v. in herb. look.)".

TYPE SPECIMENS.—*Linden* 198, G, K (Herb. look.).

Plants to 3 m tall, stems frequently branching at nearly right angles. Leaves glabrous or with a few hairs along major veins, mostly narrowly lanceolate, rarely ovate, usually attenuate at either end, occasionally somewhat falcate, the larger leaves 19(42)57 mm long, 4(7)14 broad, 4-11 serrate on a side, midrib and a few laterals standing out below. Inflorescences depressed; pedicels 1(7)14 mm long; flowers inverted. Calyx glabrous or glabrate, 10(14)18 mm long, 4(5)6 mm broad, major veins standing out, the lobes oblanceolate or narrowly triangular, frequently spreading, 6(9)15 mm long, rarely serrate. Corolla red or red-orange, 32(41)47 mm long, 5(6)8 mm broad, the upper lip 8(16)20 mm long, little or not galeate, the lobes reflexed; lobes of the lower lip 3 mm long. Stamens dimorphic, the upper pair short and rudimentary, the lower pair with expanded lamellae and shaggy anthers, the lobes short mucronate. Capsules ovoid to 12 mm long, to 8 mm broad. (Figure 34). Altitude: 1000-2800 m. Flowering: December to April, peak December to February.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 30).—MEXICO: Chiapas (13); Michoacán (doubtful—Dos Teteras, Arsené, II 1909, H); Oaxaca (between Suchixtepec and El Guajolote, Ernst & Delgadillo 2628, US). GUATEMALA: Alta Verapaz (11); El Progreso (between Jute de Cobana and Finca Piamonte, Steyermark 4368, F, PH); Guatemala (Montaña of Las Nubes west of San José de Pinula, Williams & Molina

15272, F, GH); Quezaltenango (5); Quiché (San Miguel Uspatan, Heyde & Lux, Apr. 1892, GH, US); Sacatepéquez (5); San Marcos (Volcán Tajumulco, Steyermark 36561, F); Sololá (2); Zacapa (2). EL SALVADOR: Chalatenango (Los Esimiles, Tucker 1007, F, G, MICH, PH, UC, US); Morazan (Montes de Cacaguatique, Tucker 658, F, G, MICH, PH, UC, US); San Salvador (2). COSTA RICA: Cartago (4); Puntarenas (Ujarrás, Oersted 9400, A, C, MICH, US, W); San José (11).

Floral as well as vegetative characteristics of *L. lanceolata* link it to other species in Hemispadon. It is distinguished from all other species in Hemispadon, however, by its growth habit which tends to be deliquescent, the branching frequently at right angles, the inflorescence tips depressed, and the flower inverted. This peculiar syndrome has been discussed previously for *L. xalapensis* and its closest allies in section Lamourouxia.

The plant in Oaxaca (Ernst & Delgadillo) was a low, intricately branched shrub; some other herbarium specimens look as though there were longer shoots arching over other vegetation. The elongated leaves, depressed inflorescences, and reflexed calyx lobes distinguish this species. The peculiar inflorescence characters are shared with *L. dependens*, *L. ovata*, and *L. xalapensis* of section Lamourouxia. A taxonomic problem exists with *L. integrerrima* in Guatemala partly because of variation and partly because of poorly preserved specimens.

25. *L. colimae* W. R. Ernst & M. F. Baad, Madero 20: 342. "1970," 17 March 1971.

TYPE LOCALITY.—Colima: Mountain summits near pass ca. 11 miles south-southwest of Colima on Manzanillo road; elevation 500 m. 21 September 1958.

HOLOTYPE.—*Rogers McVaugh* 18077 (& H. F. Loveland, R. W. Pippen), MICH (Figure 36).

Stems erect to 1 m tall. Leaves glabrous or with very few hairs, elliptical or ovate, 18-26 mm long, 6-10 mm broad, attenuate basally, mostly with a very short petiole or sessile, margins revolute, 3-6 serrate or dentate on a side, veining standing out below, midrib and 3-6 laterals recessed above. Inflorescence erect; pedicels 3-4 mm long. Calyx glabrous or microscopically papillate, 6-7 mm long, 4 mm broad, the lobes 4-6 mm long, broadly triangular, spreading. Corolla scarlet, 30-35 mm long, 6-7 mm broad, the



FIGURE 36.—Section Hemispadon. *L. colimae*, holotype. McVaugh 18077, MICH.

upper lip 12–13 mm long, the lobes shallow, rounded, slightly cuspidate, little or not reflexed; the lobes of the lower lip about 1 mm long. Upper pair of stamens one-half or less the length of the corolla, their anthers vestigial and glabrous; lower pair of stamens as long as the corolla, the filaments expanded distally, the

anthers shaggy pubescent, their lobes short acuminate at base. Style with a few short hairs. (Figure 34).

DISTRIBUTION.—MEXICO: Colima (see type; and also see Figure 30).

This species is known only from the type collection. It seems close to *L. lanceolata*, although the inflores-

ence is erect, somewhat similar to *L. gracilis* although the corollas are narrower, and recalls *L. gutierrezii* although the leaves are glabrous. The low altitude seems notable.

6. *L. gutierrezii* Oersted in Bentham & Oersted, Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjöbenhavn for Aaret 1853: 29. "1854," but the first part, including p. 29, probably distributed in 1853.

TYPE LOCALITY.—"Denne smukke Art voxer i den ppige Skov, som beklæder Bjergene mellem Cartago og Candelaria i en Höide af 6—7000 Fod, hvor jeg af den med Blomst i Februar."

TYPE SPECIMENS.—Costa Rica, "Inter Cartago et andelaria, 8000', 2/47," Oersted 9398, C; ? "No. 3, In monte Candelaria," K (Herb. Benth.).

SYNONYMY.—

L. scabra Bentham ex Seemann in Bot. Voy. H.M.S. Herald, p. 177. pl. 33. 1854. Type locality: "Volcano of Chiriquí, Veraguas." Type specimens: Panama, Seemann, Bot. Herald, tab. 33, "to be figured," BM; Seemann, Boquete, Mar. 1848, K (Herb. Benth.).

Stems erect to 2 m long. Leaves scabrous pubescent, elliptical to ovate, 8(15)25 mm long, 4(6)10 mm broad, usually tapered below, petiole to 2 mm long, margins serrate to crenate with 4 to 10 teeth on a side; veining standing out below with 1 or 3 principal veins, usually recessed above. Inflorescences ascending; pedicels 2-3(4) mm long. Calyx pubescent, (8)10 mm long, 4-5 mm broad, the lobes 2(3)4 mm long, broadly triangular, occasionally incised. Corolla (orange or ?yellow), 32(37)44 mm long, 4(6)8 mm broad, the upper lip 12(15)18 mm long, slightly not at all galeate, the lobes reflexed; the lobes of the lower lip 1-2 mm long. Stamens dimorphic, the upper pair rudimentary, the lower pair with thickened filaments and shaggy anthers with mucronate lobes. Capsules ovoid to spheroidal, 9-13 mm long, 7-8 mm broad. (Figure 34). Altitude: 945-1750 (2000) m. flowering: October to April and June to July, peak December to January and July.

DISTRIBUTION AND NUMBER OF COLLECTIONS EXAMINED (Figure 30).—COSTA RICA: Alajuela (5); Cartago (3); Heredia (2); Puntarenas (2); San José (1). PANAMA: Chiriquí (7).

This species is distinguished by its far southern distribution in Central America, being the only one

restricted to Costa Rica and Panama. In a general way, it seems close to *L. colimae*, *L. gracilis*, and *L. lanceolata* but is very pubescent and scabrous, thus resembling the *L. viscosa* complex; the species differs, however, in being without glands and the leaves are tapered to the base.

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